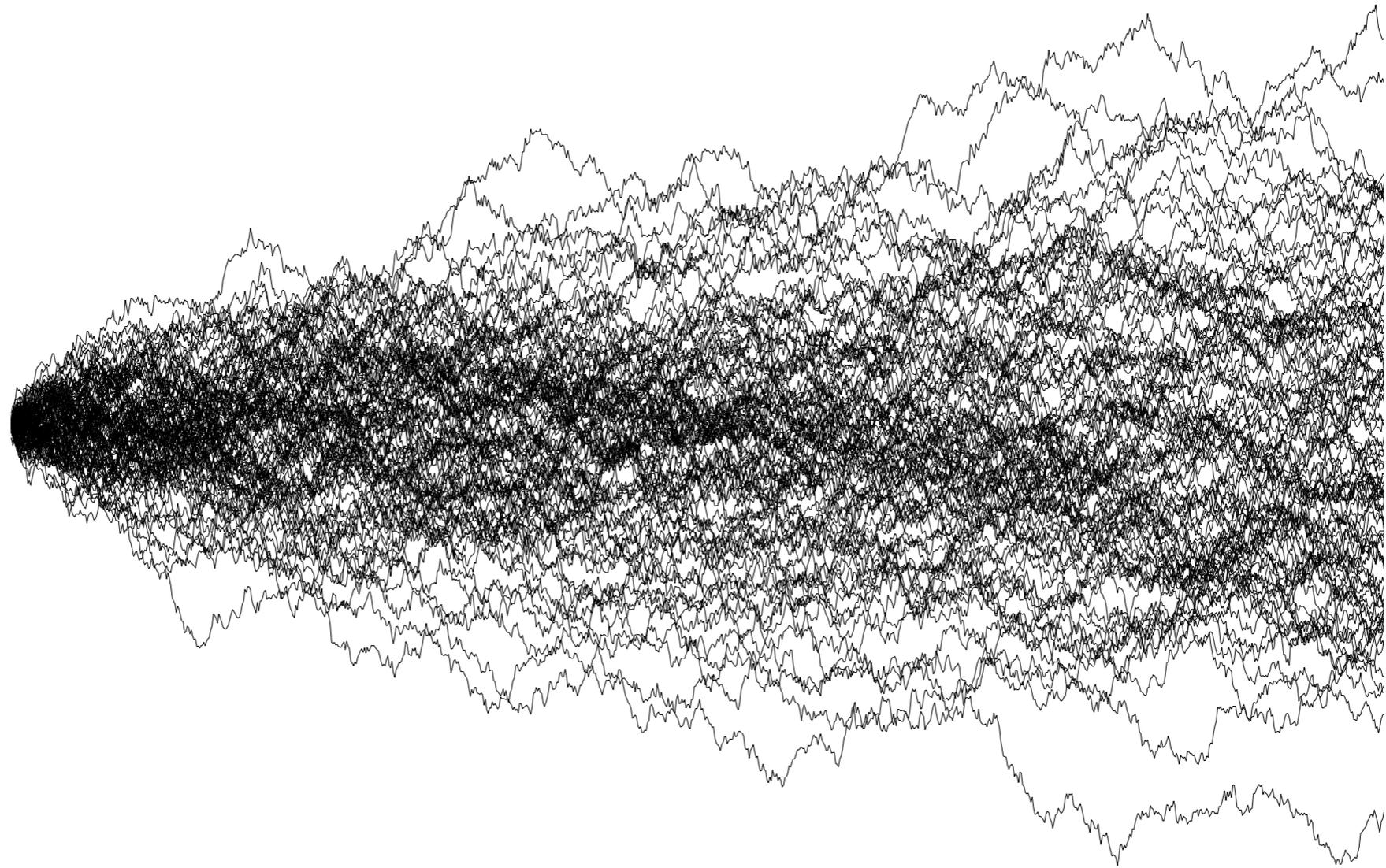


Learning outcomes

- describe Brownian motion model and explain how it is used in evolutionary analyses
- explain why species level comparisons are affected by phylogeny
- understand the contrasts procedure

Brownian Motion



What is Brownian motion?

Brownian Motion: The Model

- Describes a “random walk” of evolution for continuously-valued characters

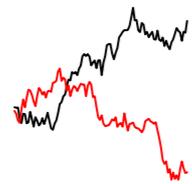
Three Facts Describe Brownian Motion

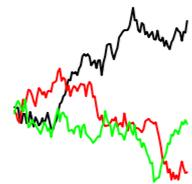
- No trend
- Successive steps independent
- Expected values follow normal distribution where variance depends on rate and time

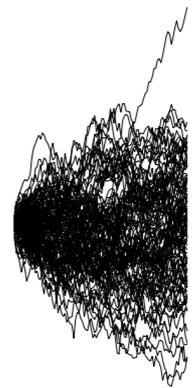
Parameters of BM

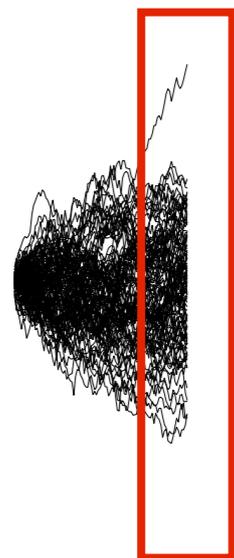
- Brownian motion models have two parameters:
 - Θ , the starting value; $W(0) = \Theta$
 - σ^2 , the rate parameter

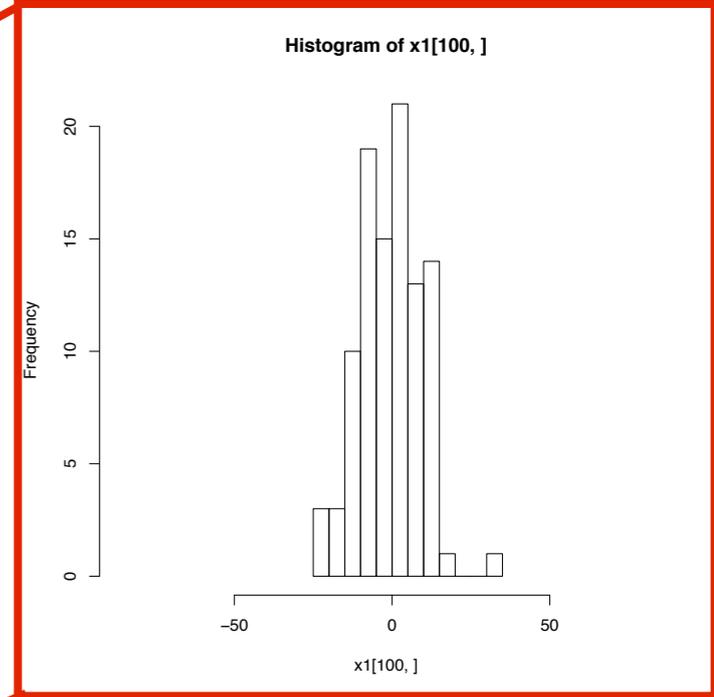
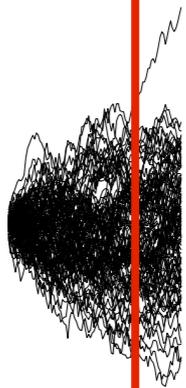
A small, handwritten scribble consisting of several jagged, overlapping lines that form a roughly upward-sloping shape. The lines are black and appear to be drawn with a pen or marker on a white background.



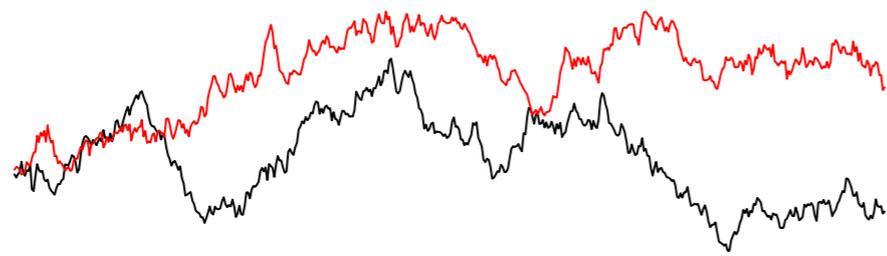


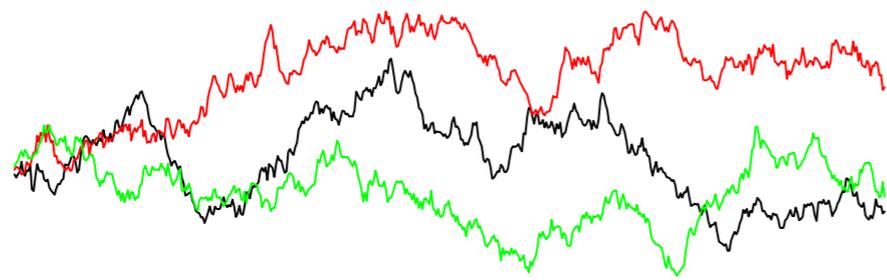


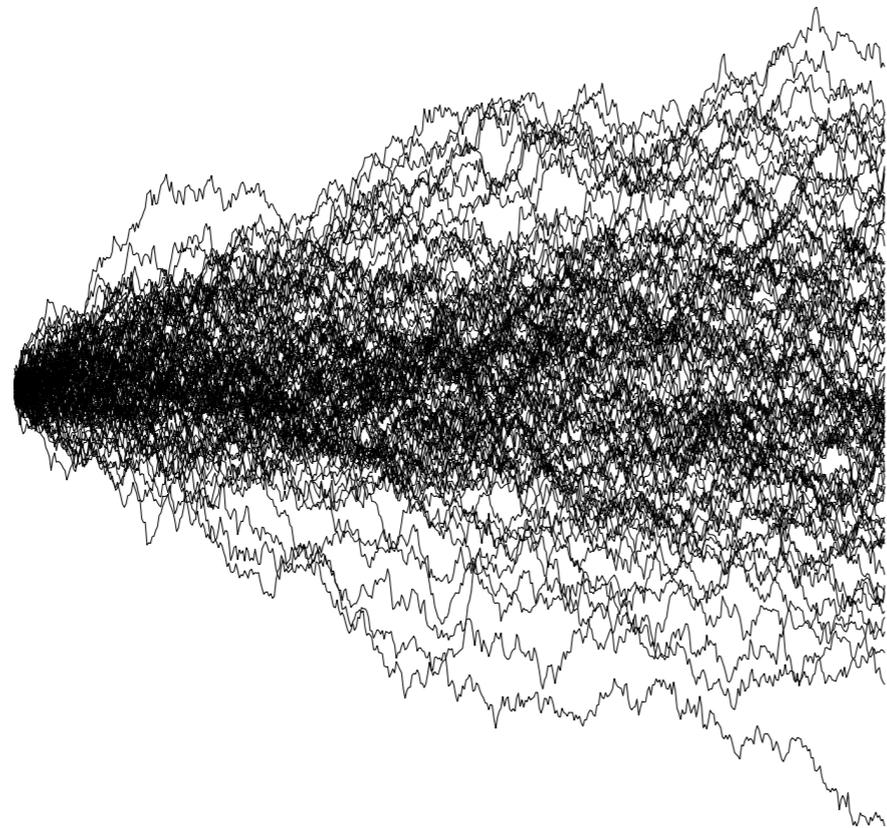


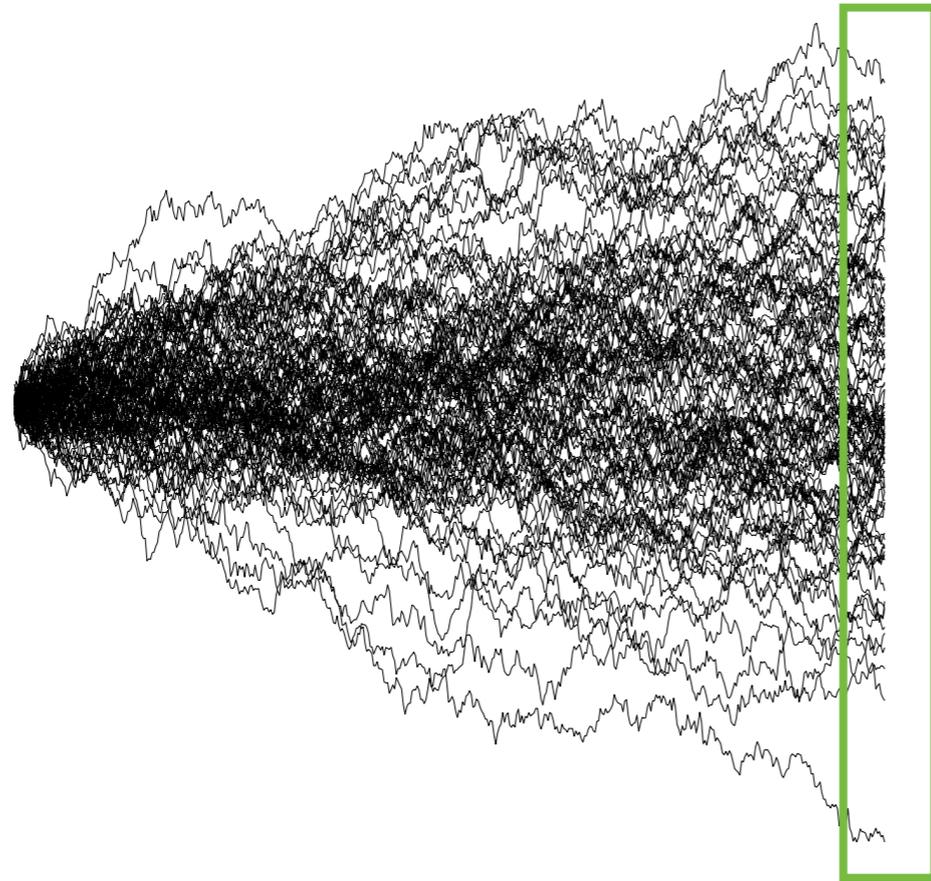


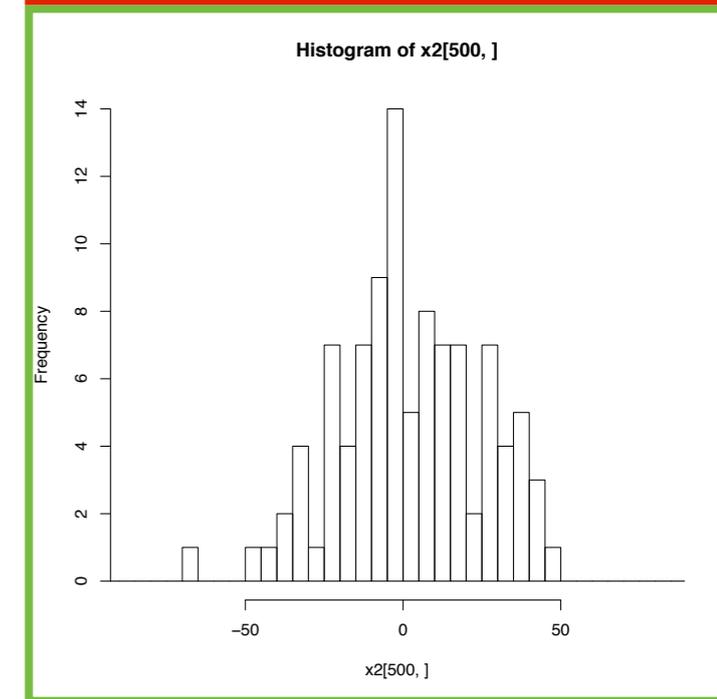
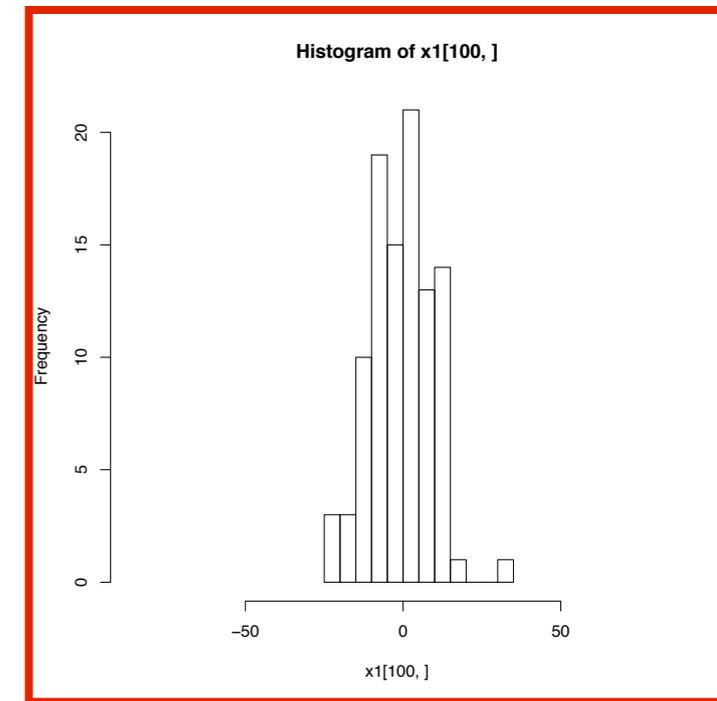
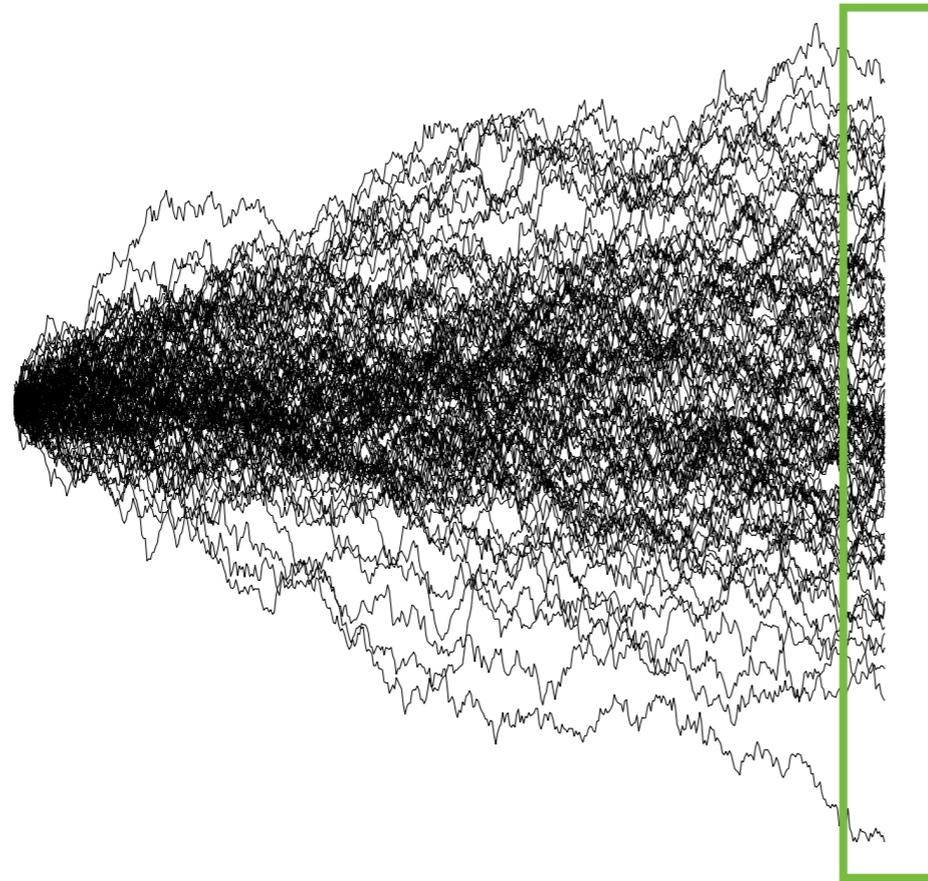


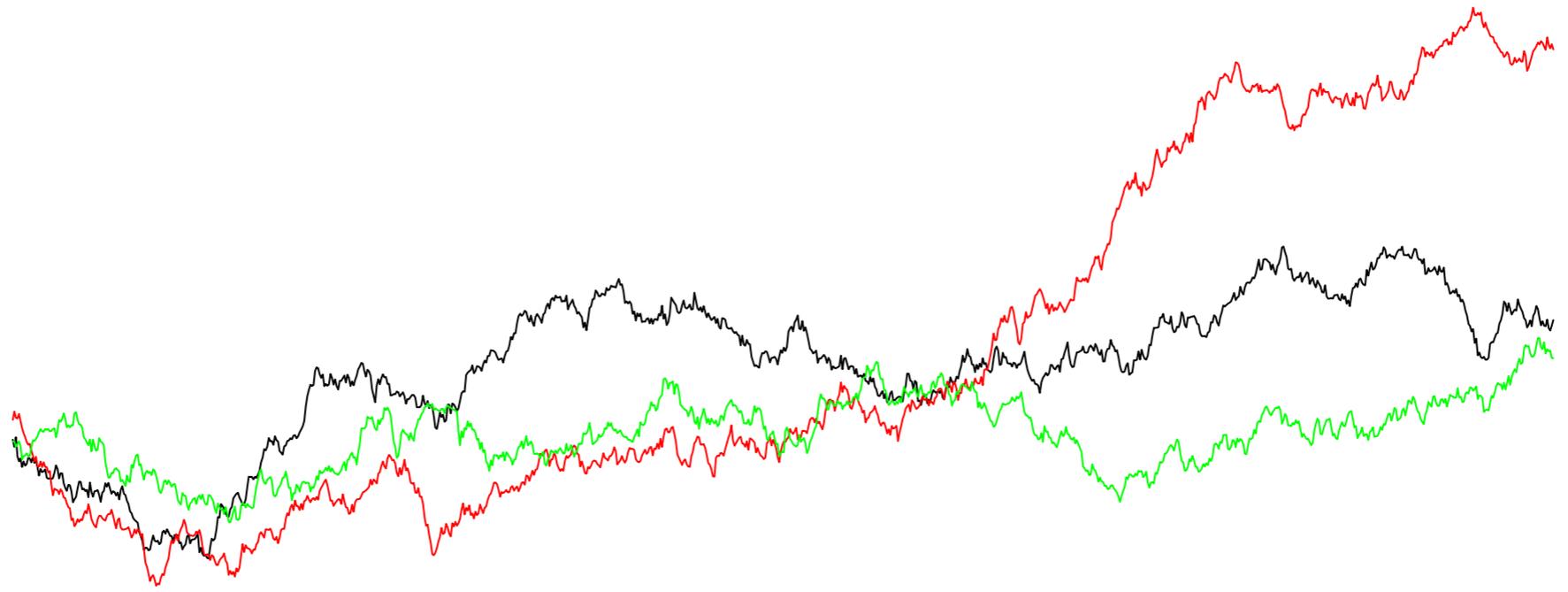


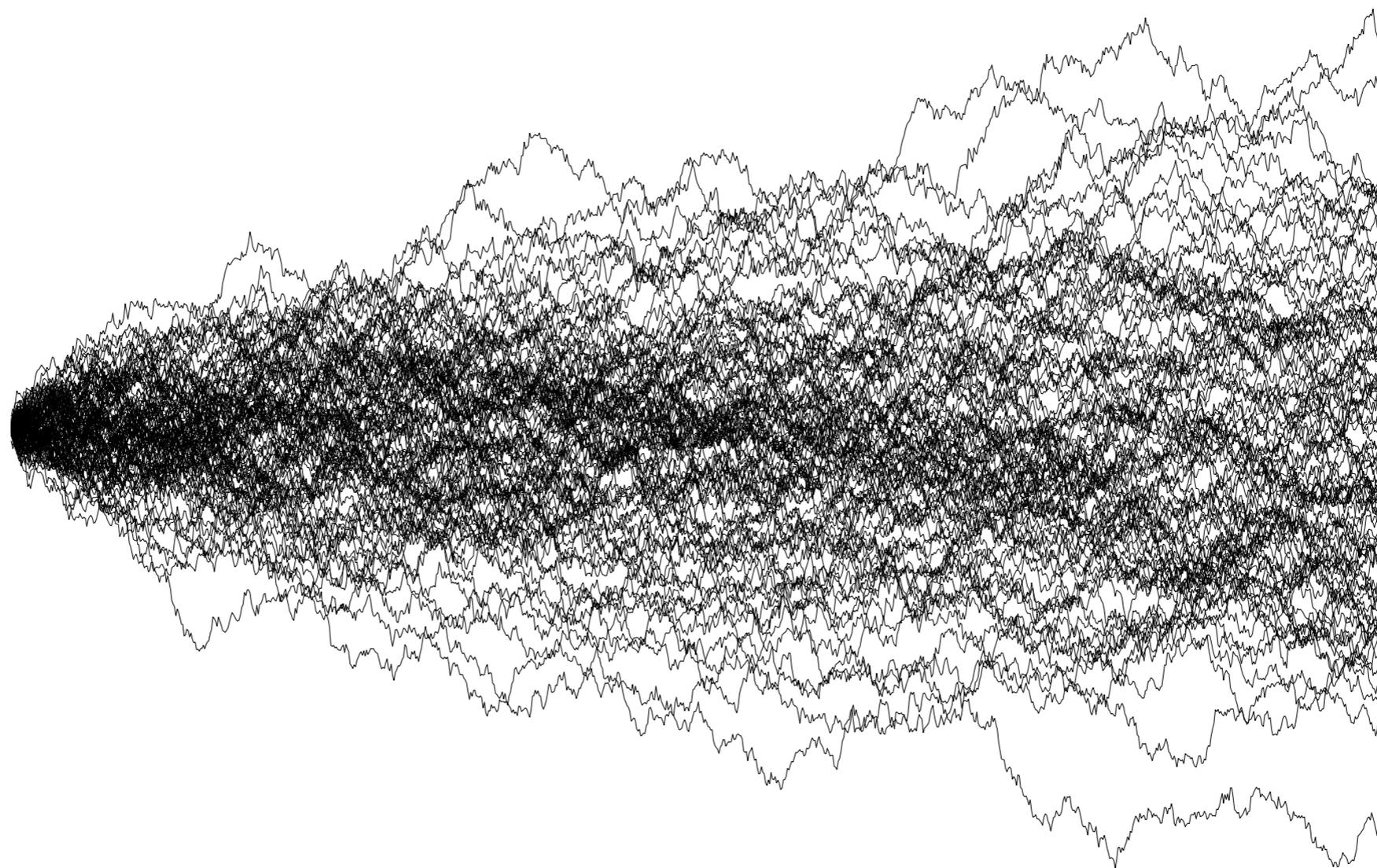


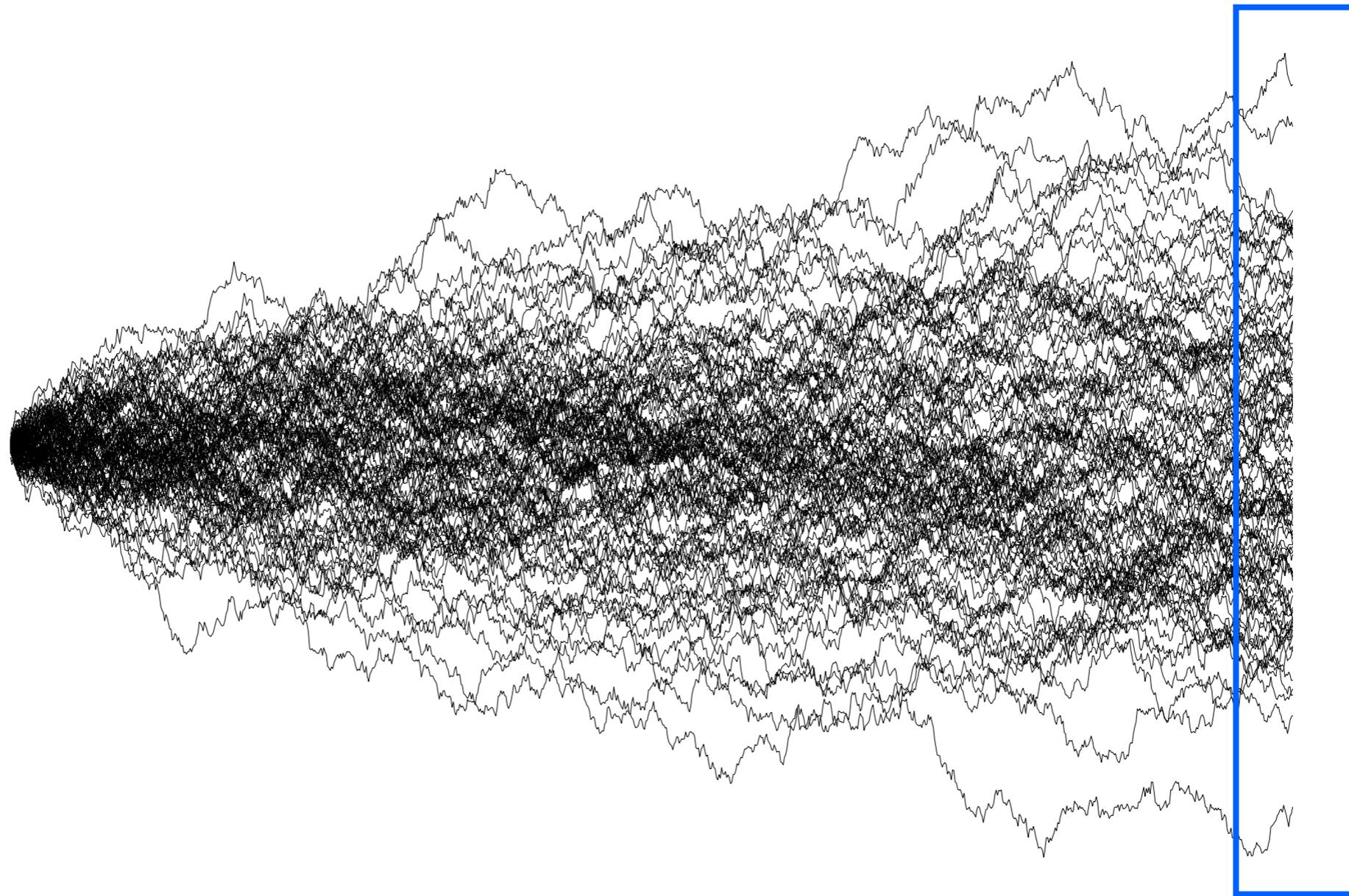


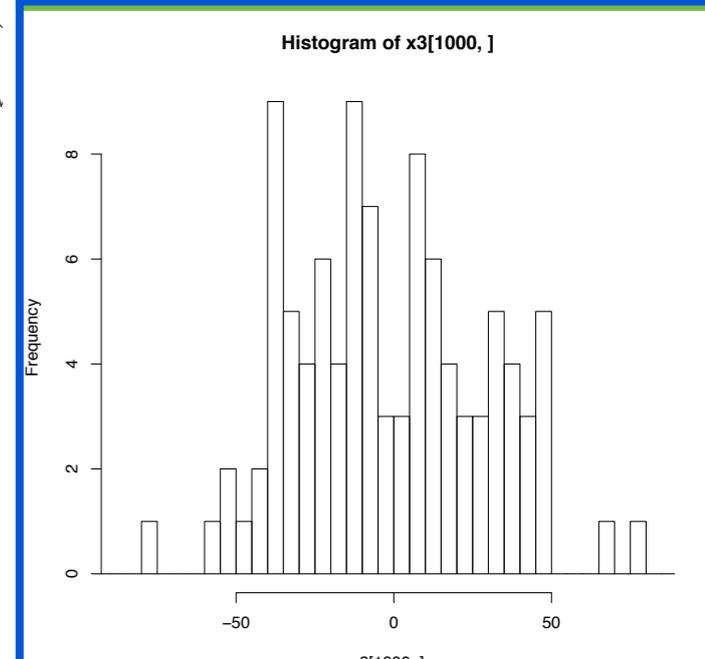
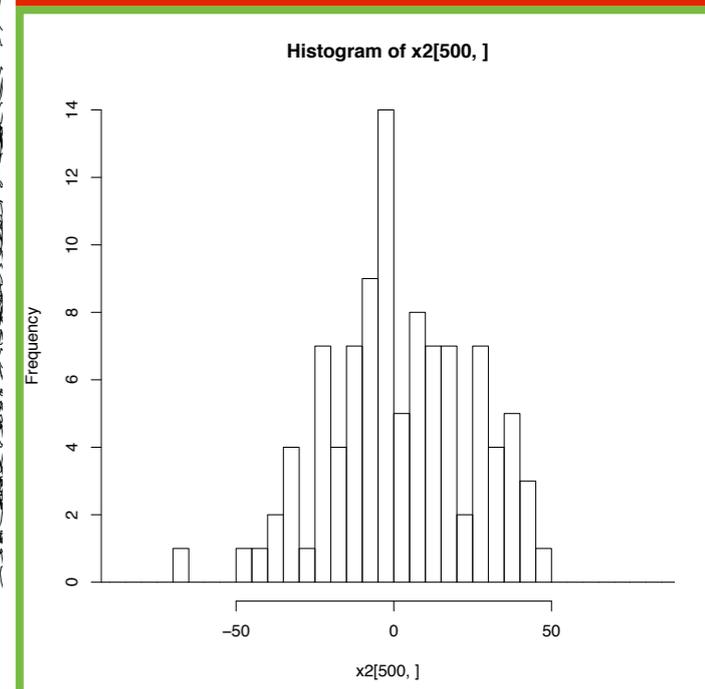
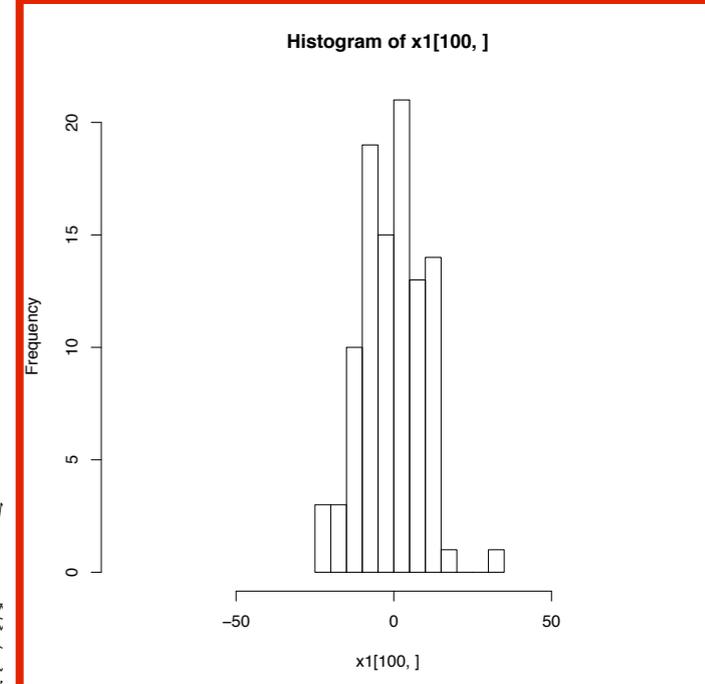
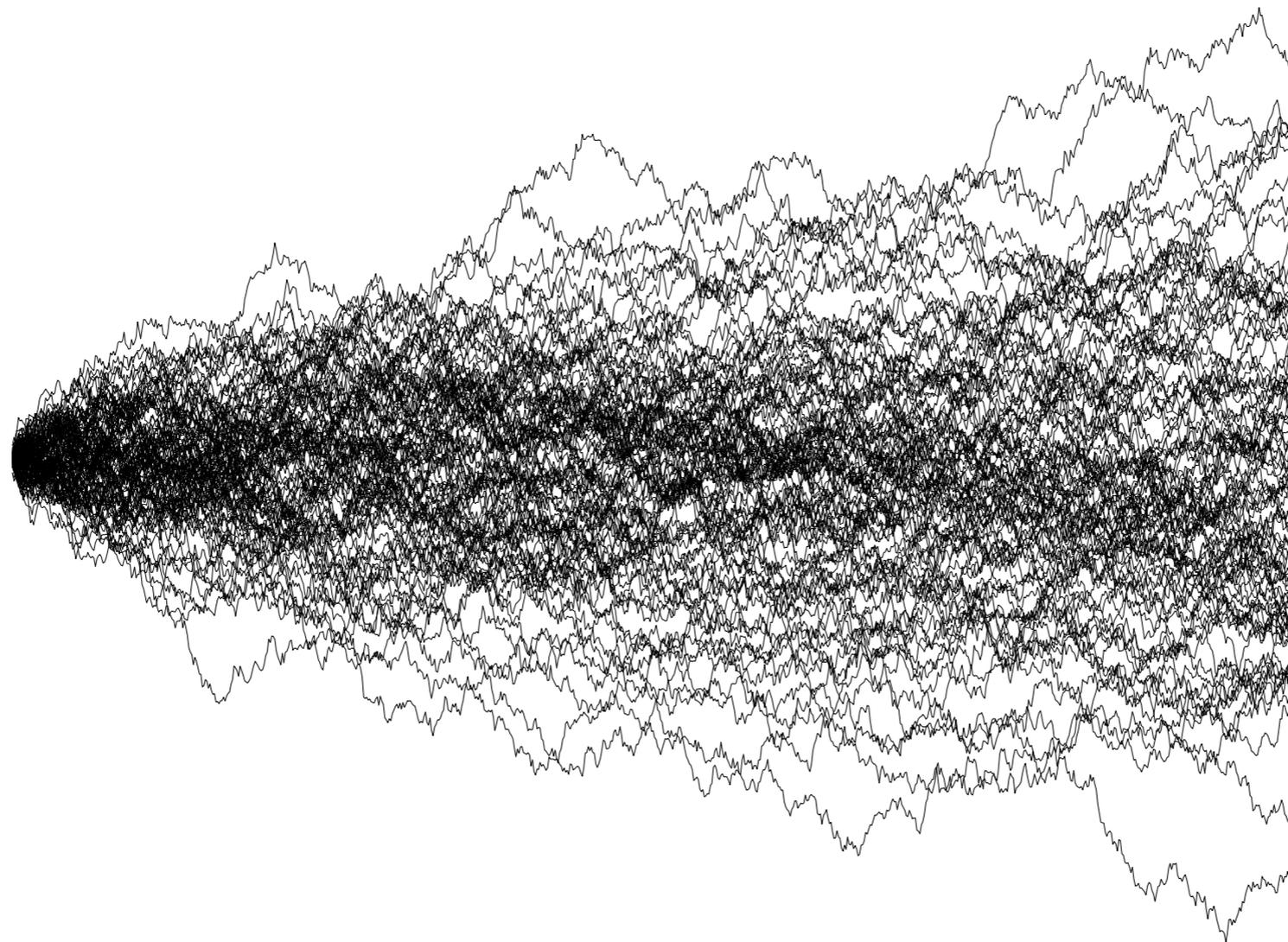




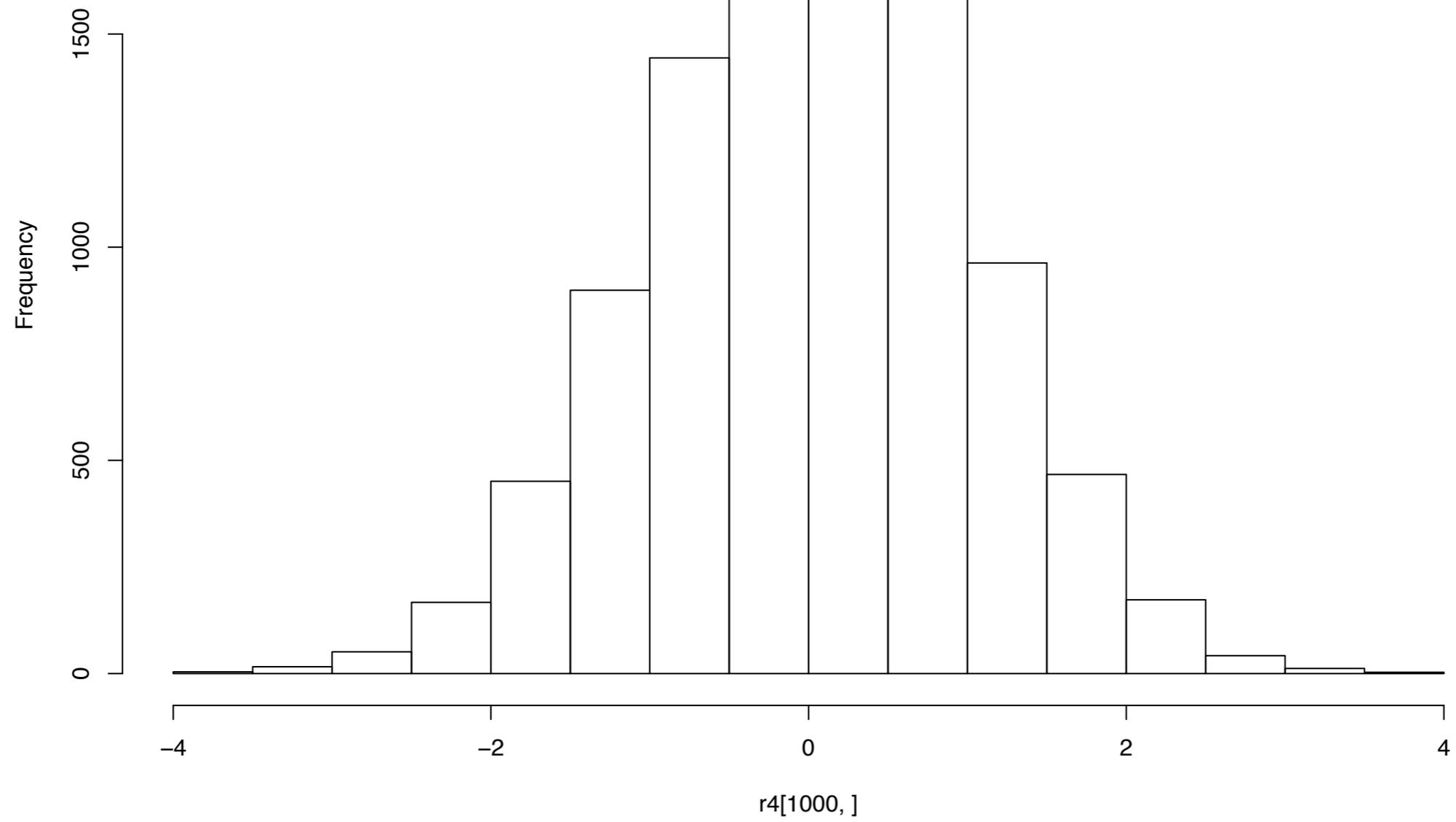


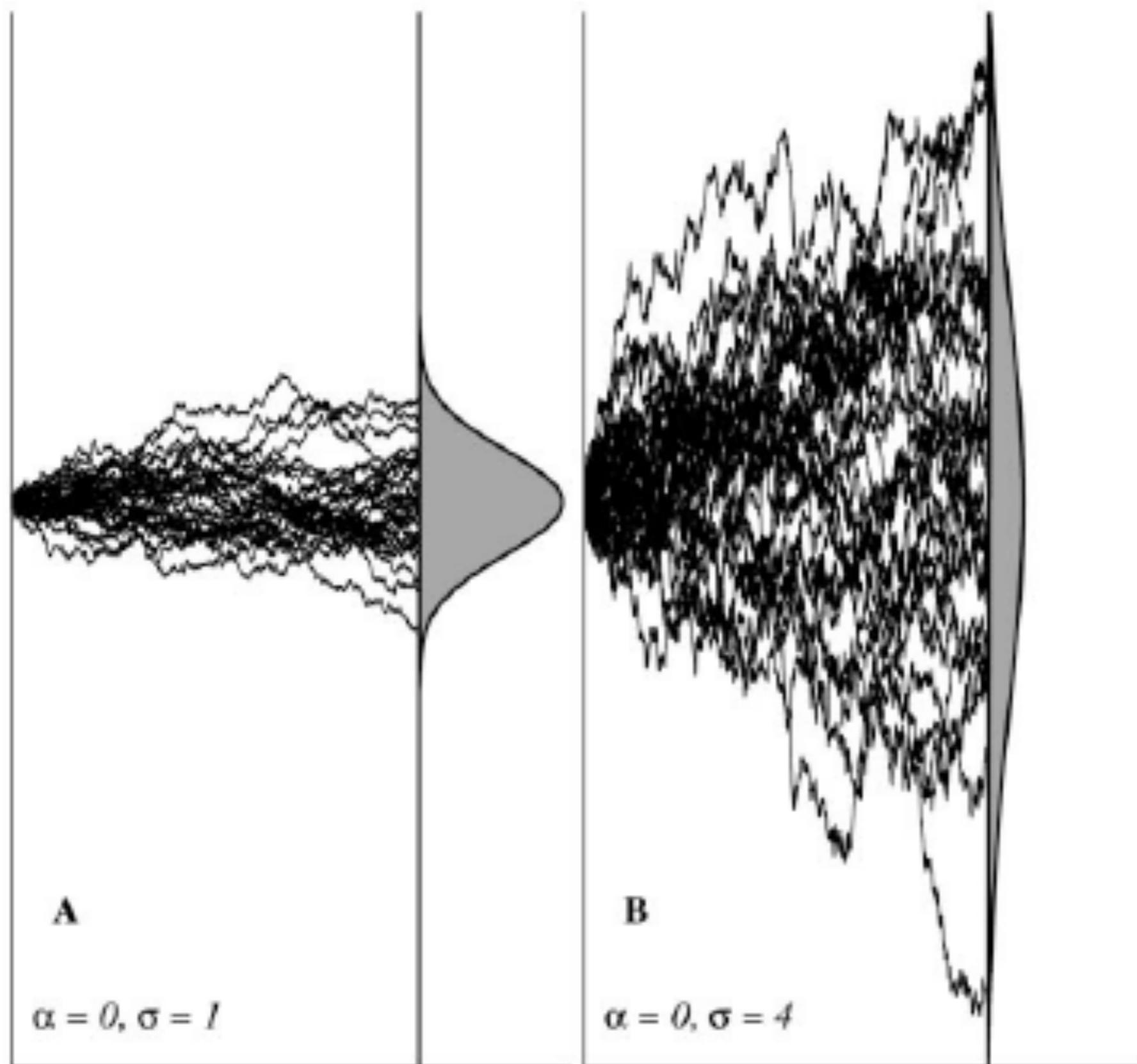






Histogram of r4[1000,]





**Why use this model
for trait evolution?**

A physical model for BM



Why Normal?

- BM can be used to describe motion that results from the combination of a large number of independent weak forces
- Adding many small independent variables result in normal distributions, no matter the original distribution (Central limit theorem)

Evolution might approximate BM...

- Genetic drift
- Random punctuated change
- Selection that is weak relative to the time interval considered
- Selection that changes randomly through time

Why are close relatives similar
to one another?

Motivation-work with partner

- How could you use the trait information from the observed species to draw an inference about body size in the ancestral species?
- What is your best estimate of ancestral body size? How confident are you in this estimate? Explain.
- Discuss how the following would (or might) impact your confidence around your estimate of ancestral body size: time since divergence, ecological constraint, fossil observations



1100 kg



950 kg

Motivation

- species pairs share a common ancestor



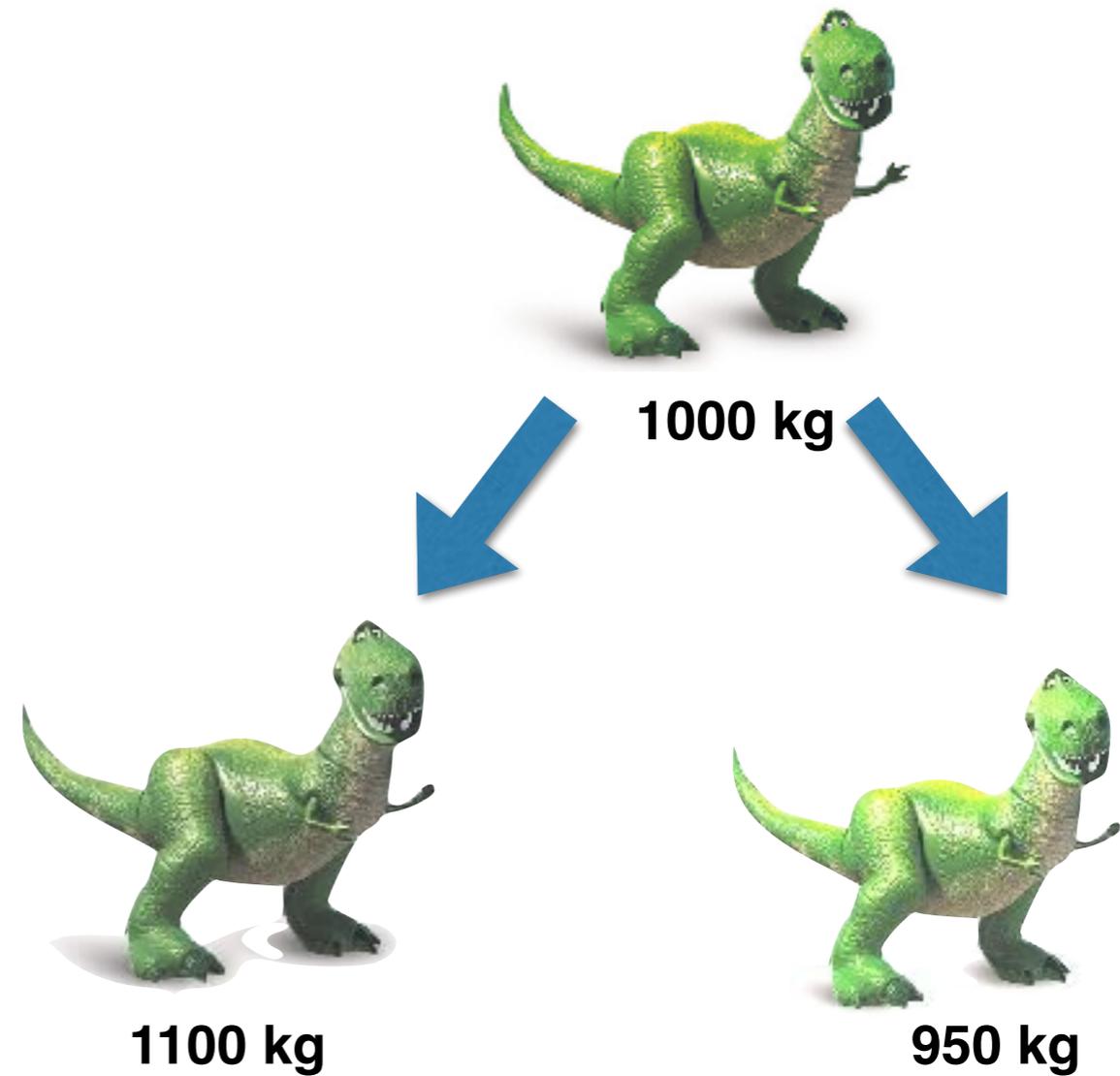
1100 kg



950 kg

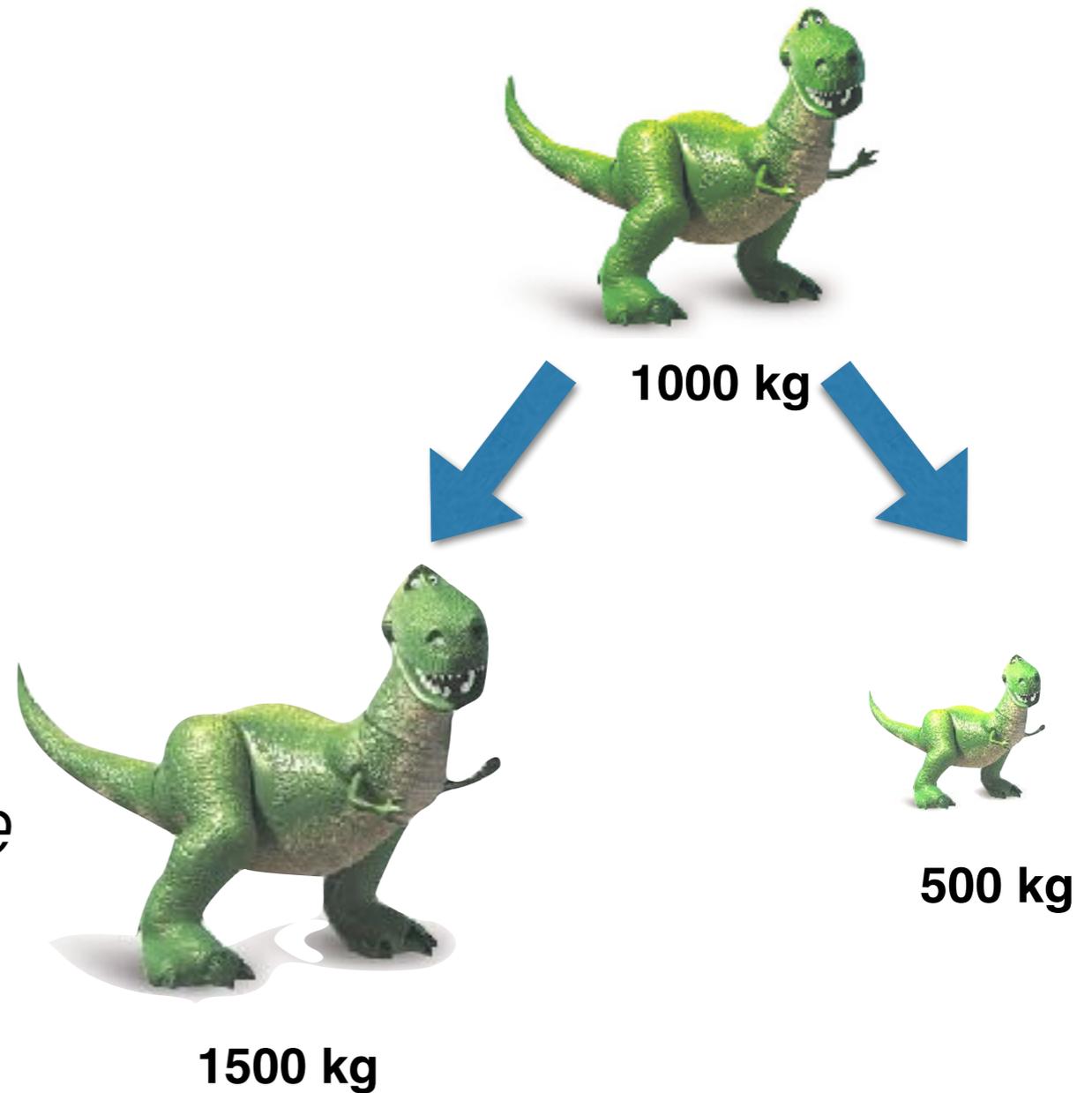
Motivation

- species pairs share trait value at ancestor



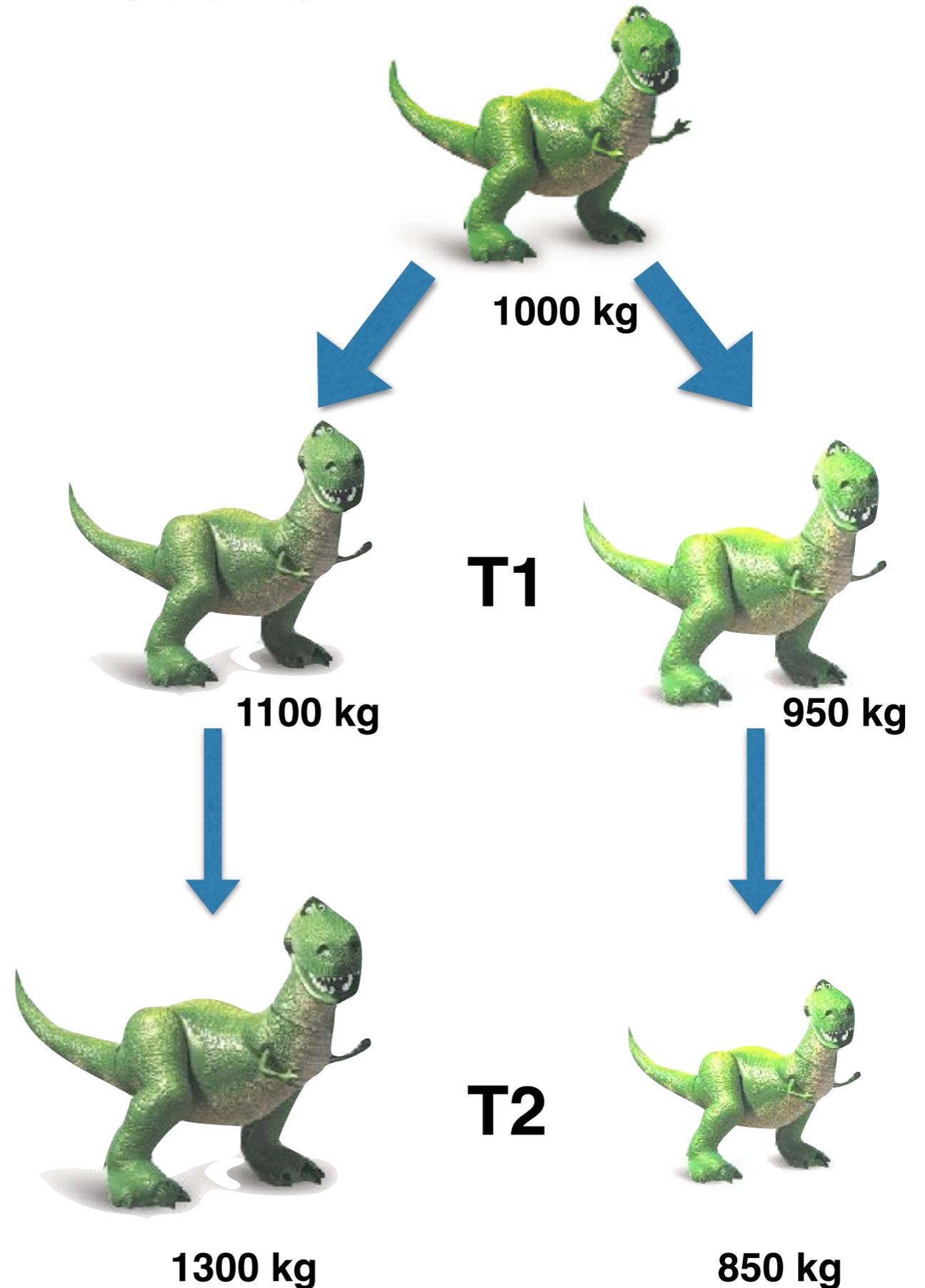
Motivation

- species pairs share trait value at ancestor
- with time since divergence, *difference* should increase



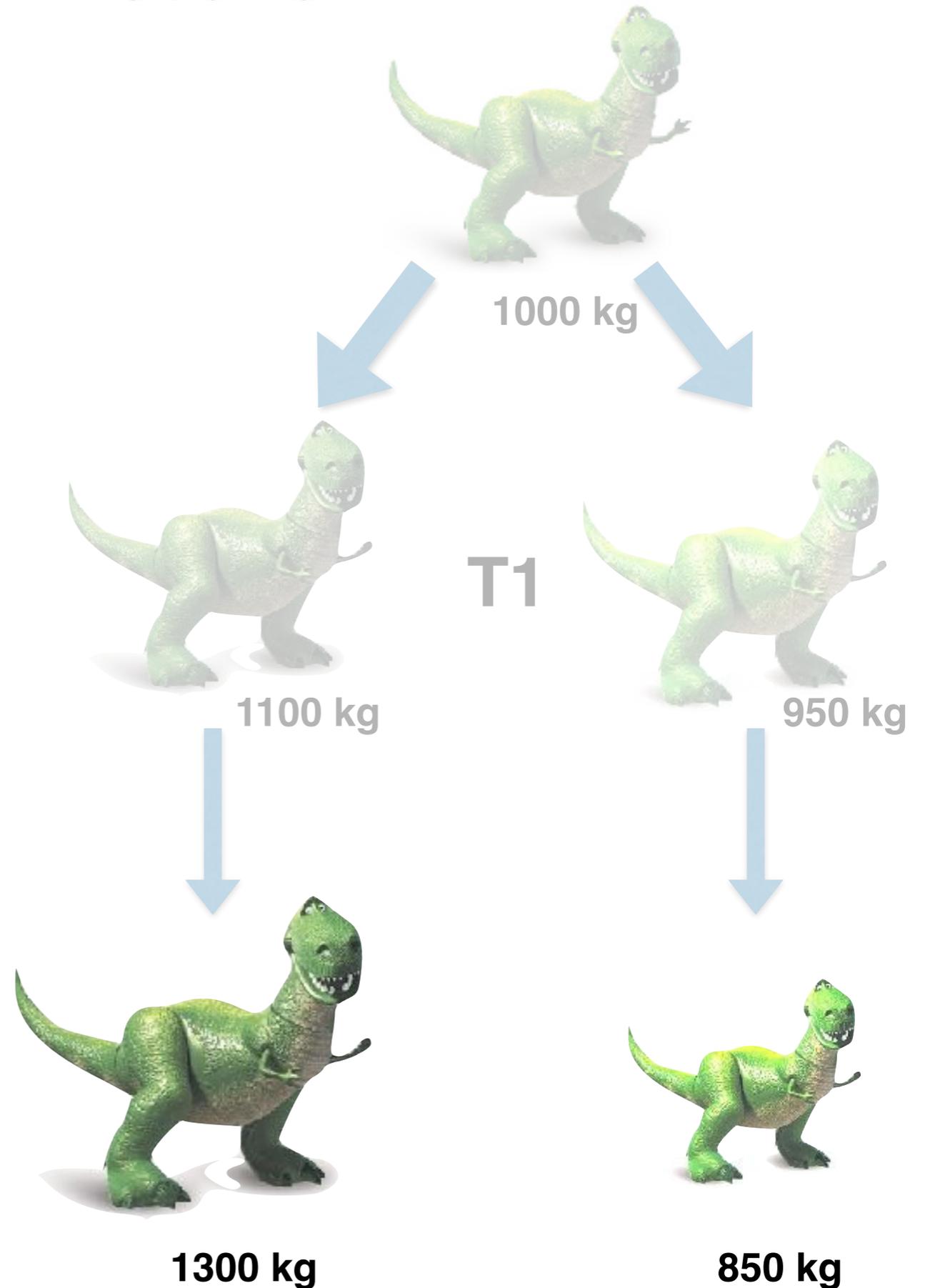
Motivation

- species pairs share trait value at ancestor
- with time since divergence, *difference* should increase



Motivation

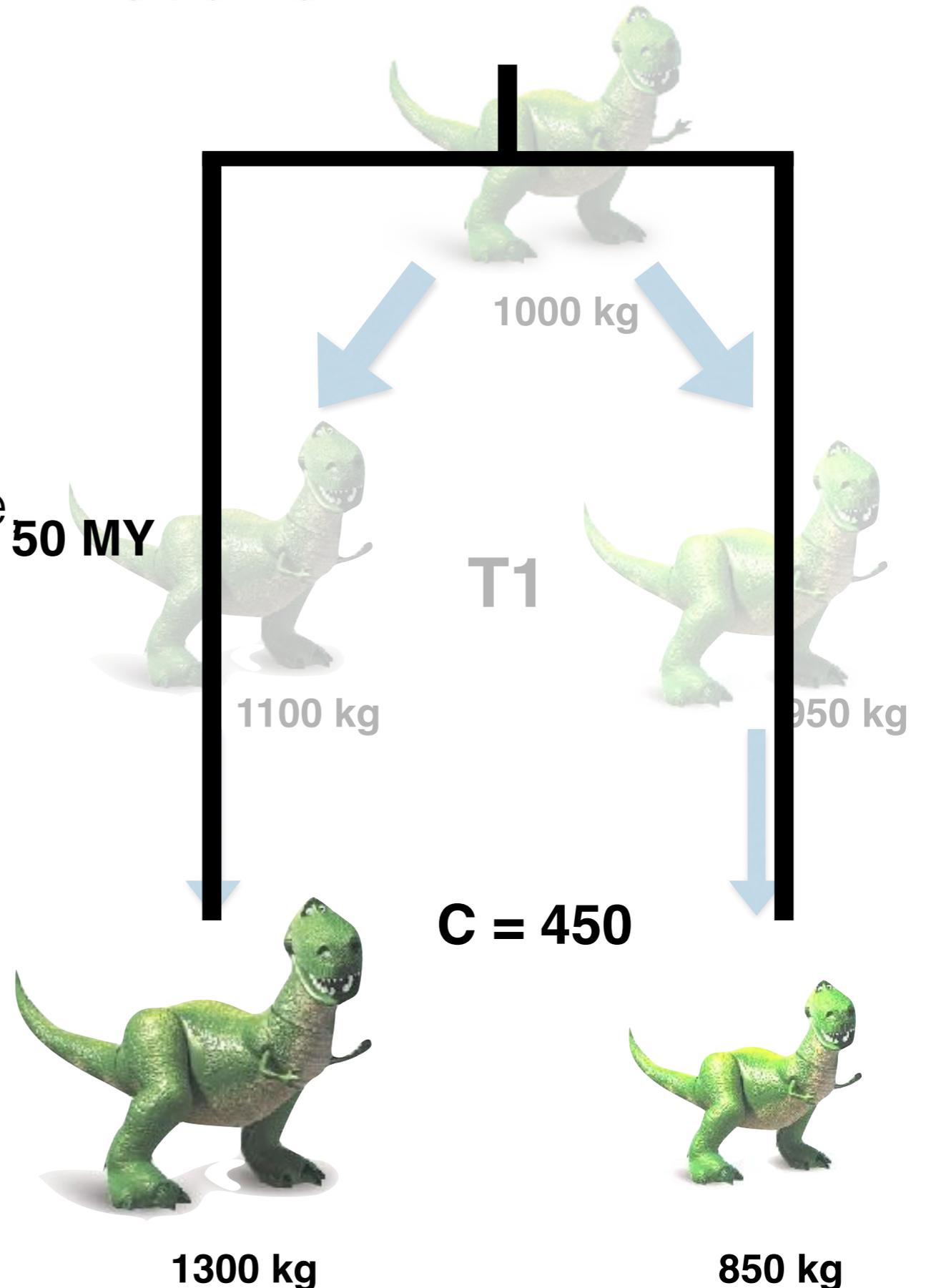
- a contrast tells you how much difference has evolved since shared common ancestor



1300 kg - 850 kg

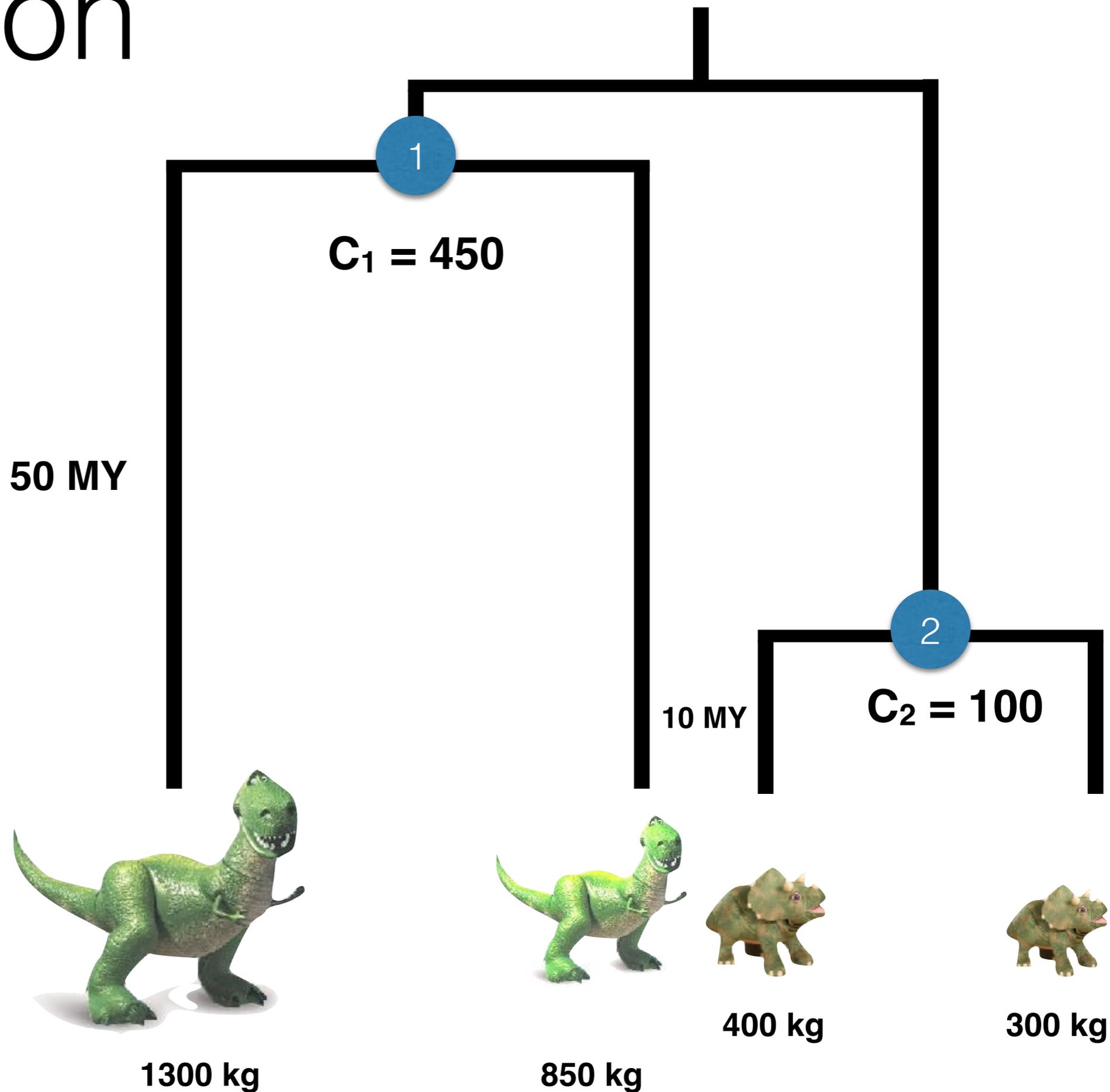
Motivation

- species pairs share trait value at ancestor
- with time since divergence *difference* should increase
- a contrast tells you how much difference has evolved since common ancestor
- (with branch lengths, we can learn about **rate**)



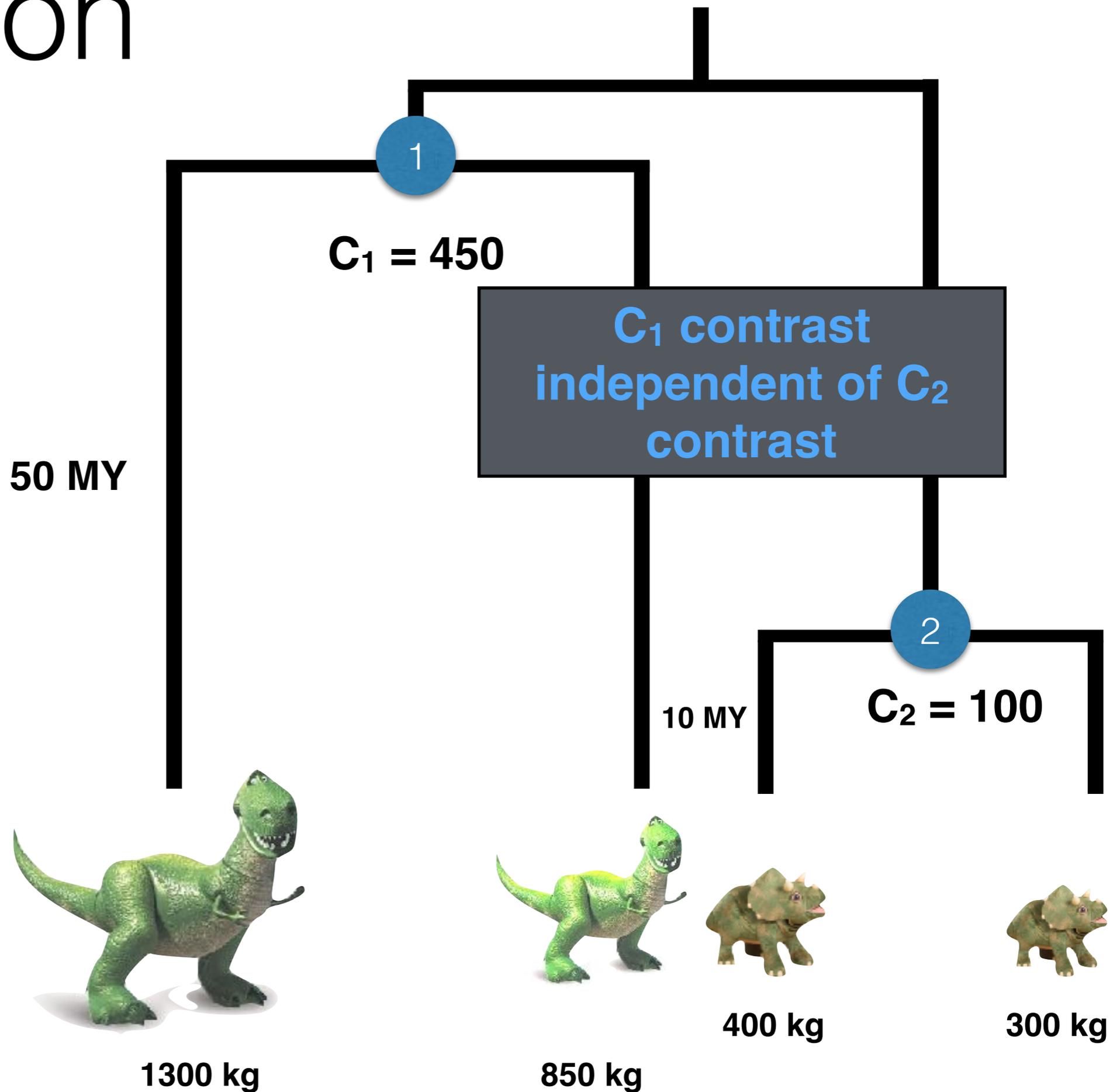
Motivation

- a contrast tells you how much difference has evolved
- contrasts from other subclades provide *independent* measures of evolutionary rate

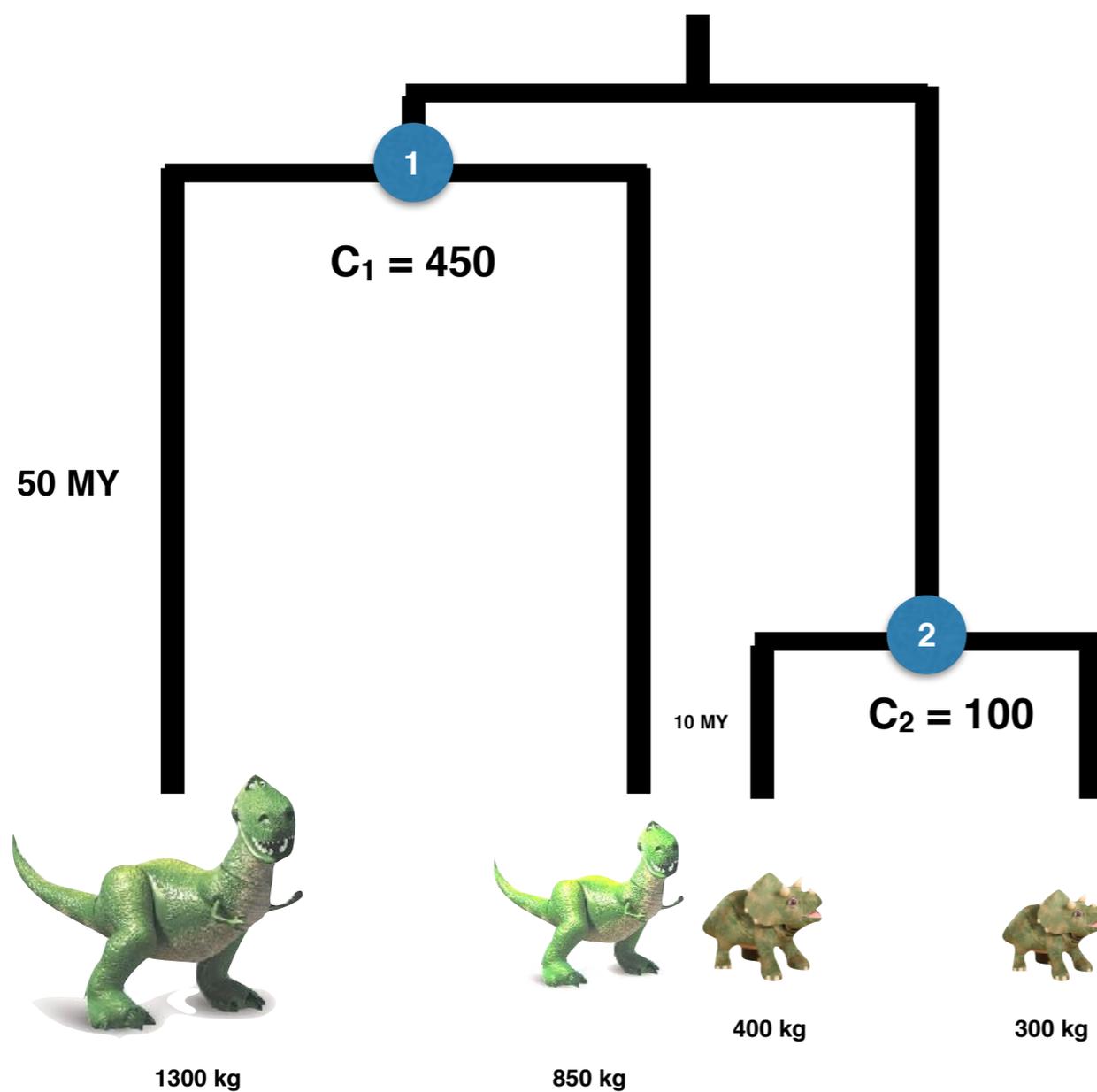


Motivation

- a contrast tells you how much difference has evolved
- contrasts from other subclades provide *independent* measures of evolutionary rate

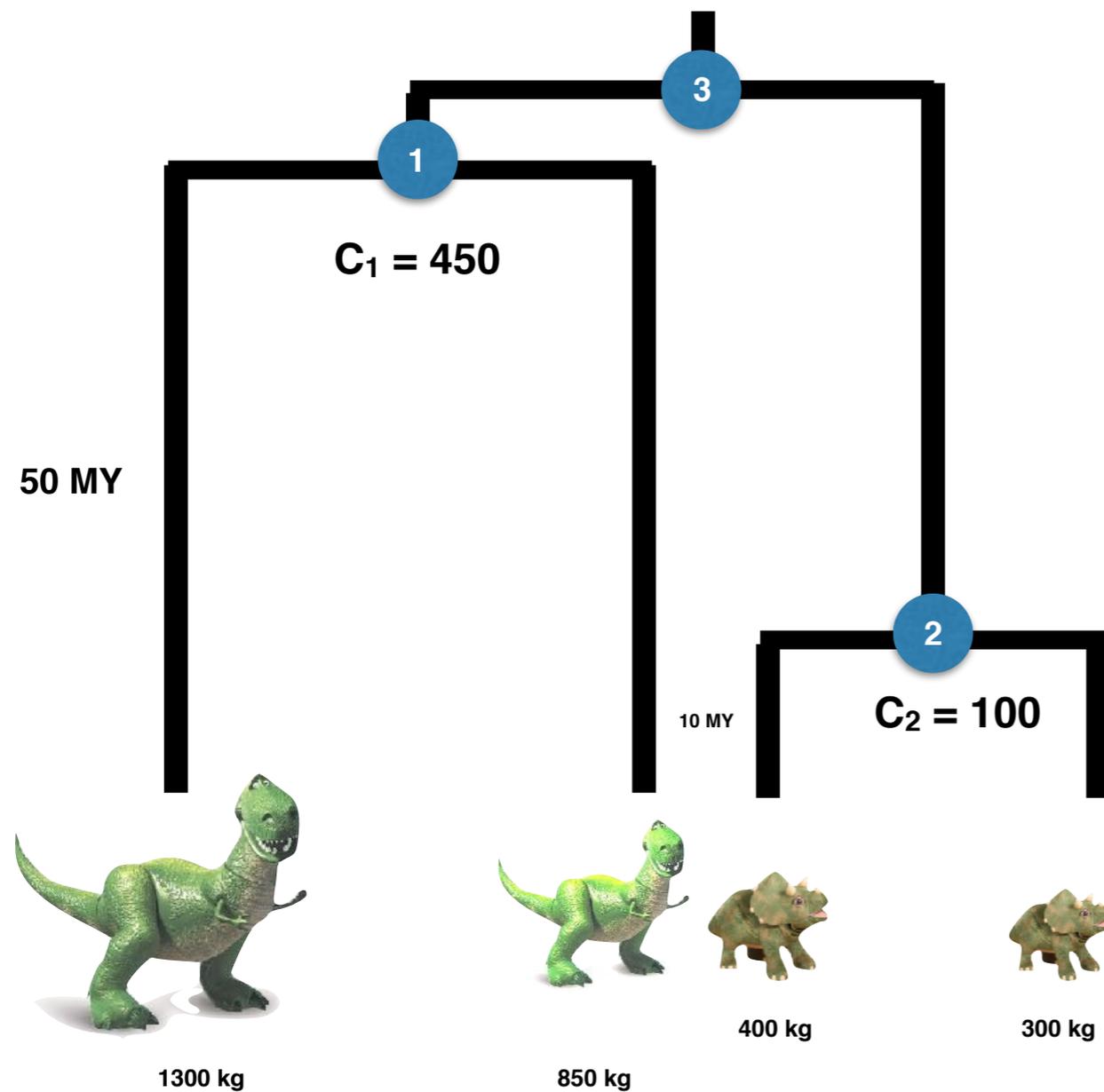


Any phylogenetic tree with N tips provides for N-1 independent contrasts



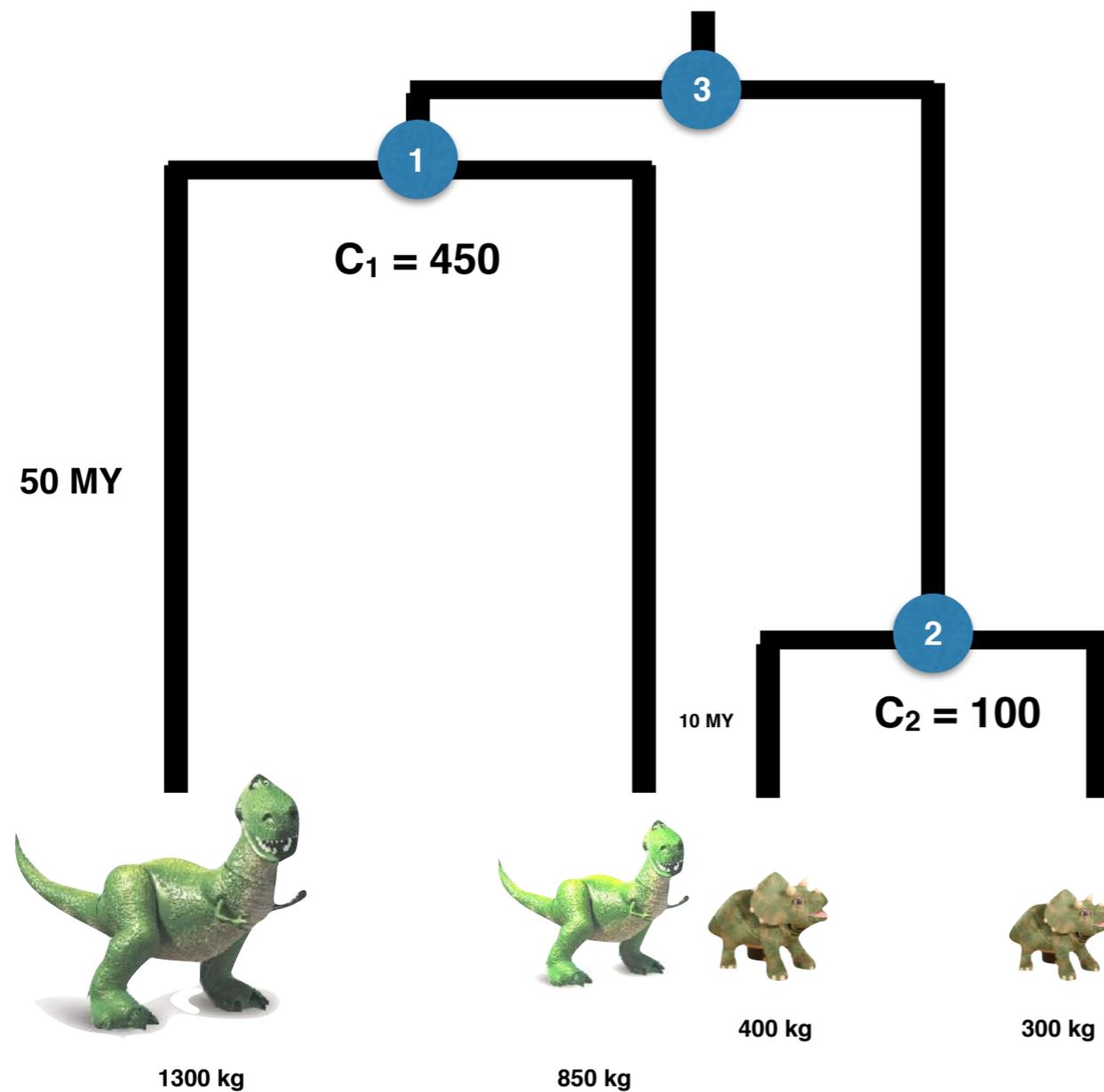
where is the third contrast?

Any phylogenetic tree with N tips provides for N-1 independent contrasts



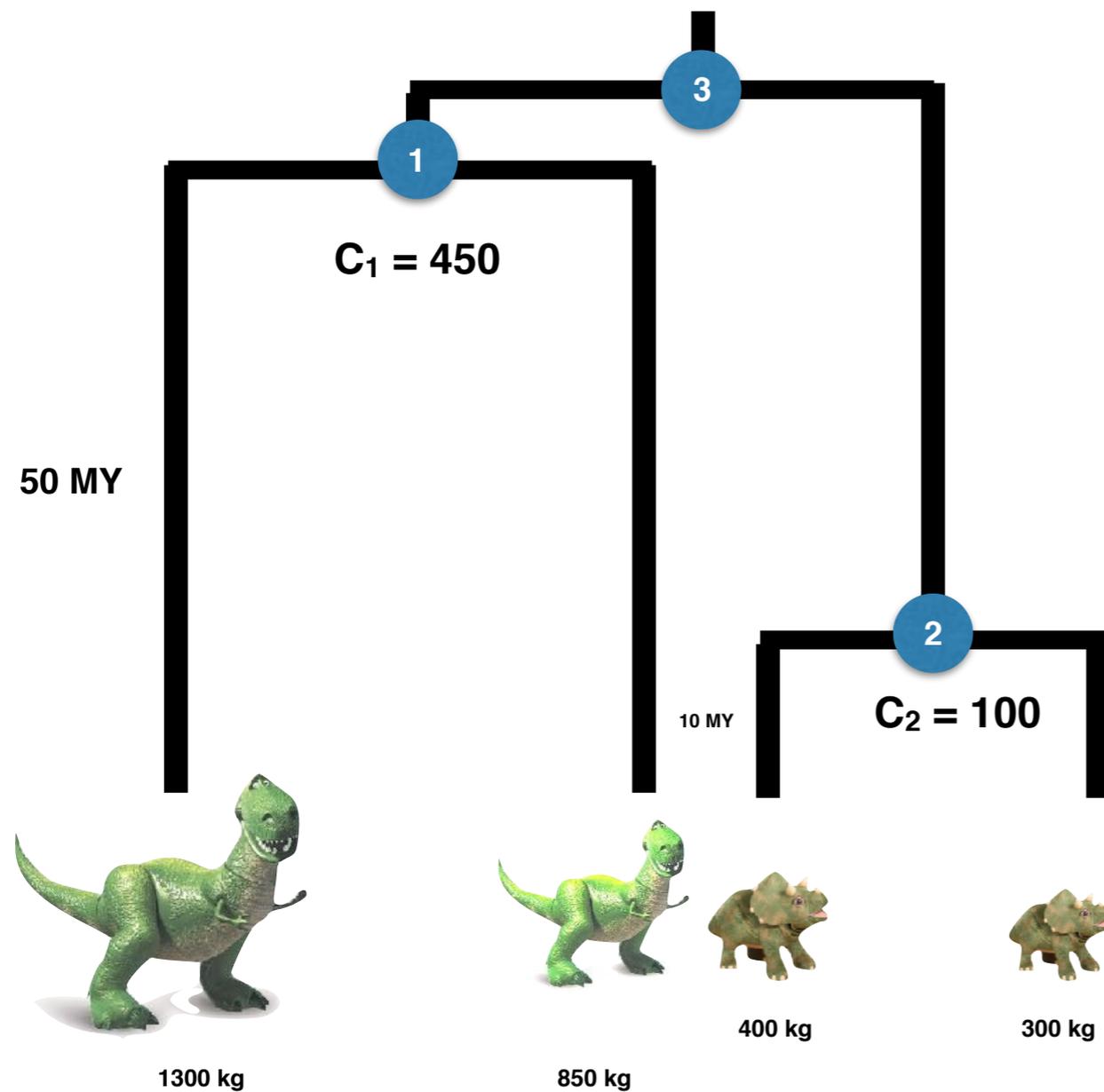
what is unusual about this contrast?

Any phylogenetic tree with N tips provides for N-1 independent contrasts



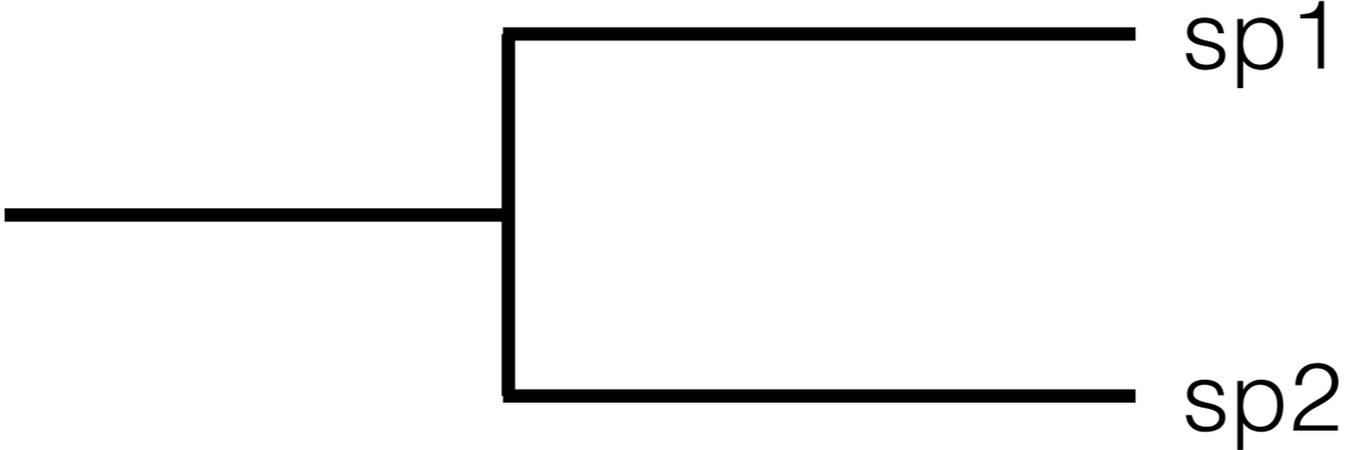
C_3 is contrast in values between (unobserved) species value of node 1 and (unobserved) species value of node 2

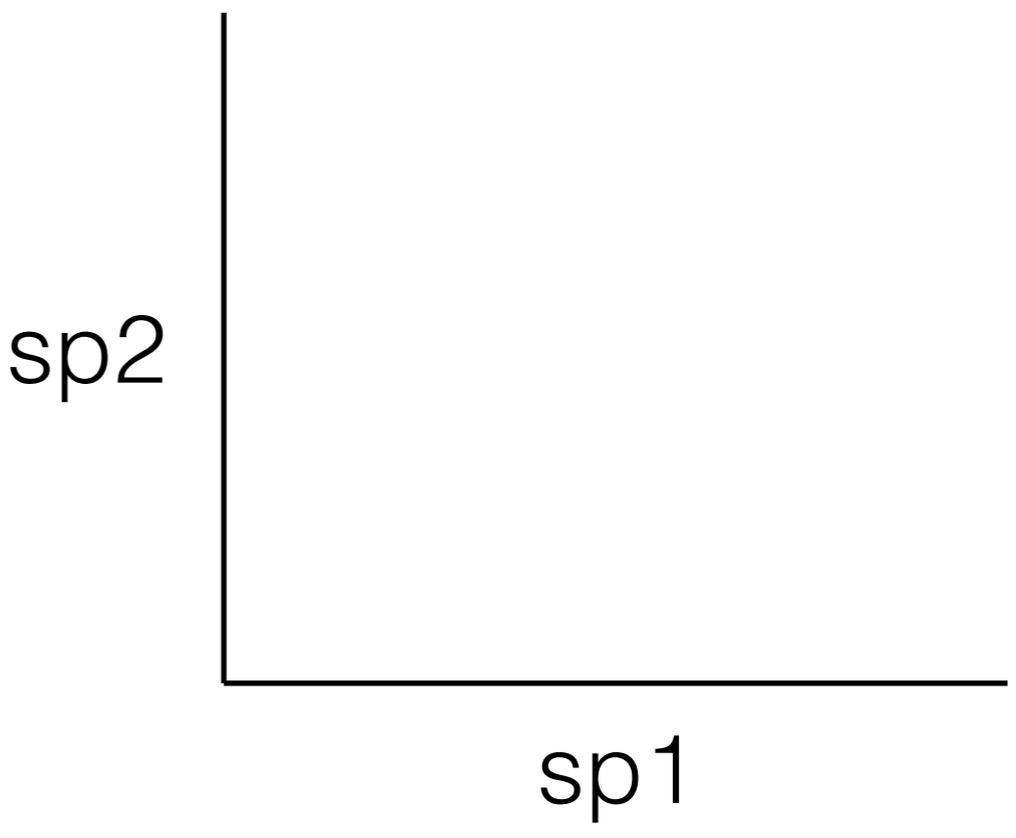
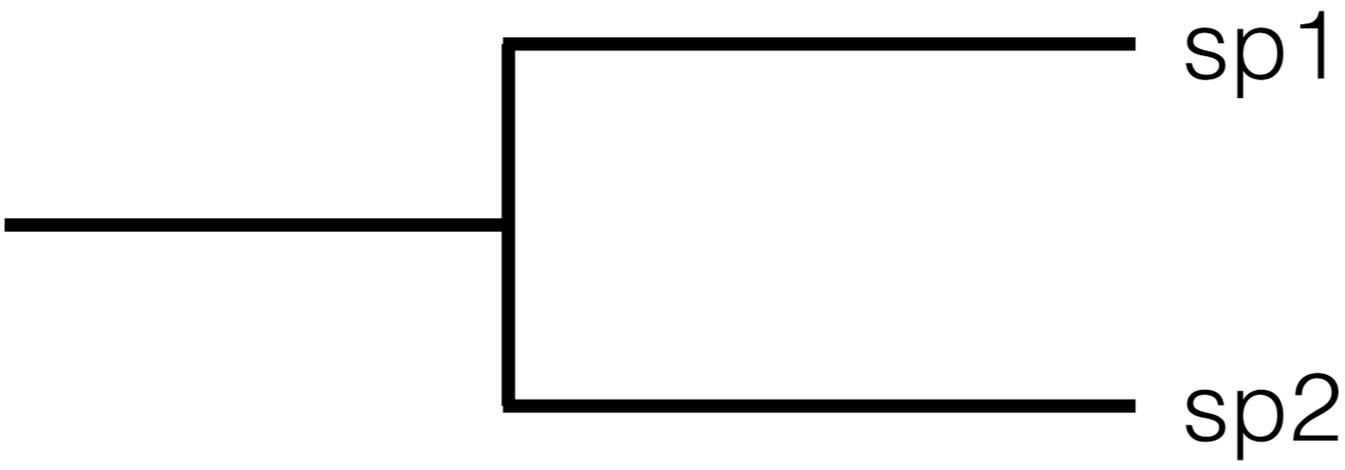
Any phylogenetic tree with N tips provides for N-1 independent contrasts

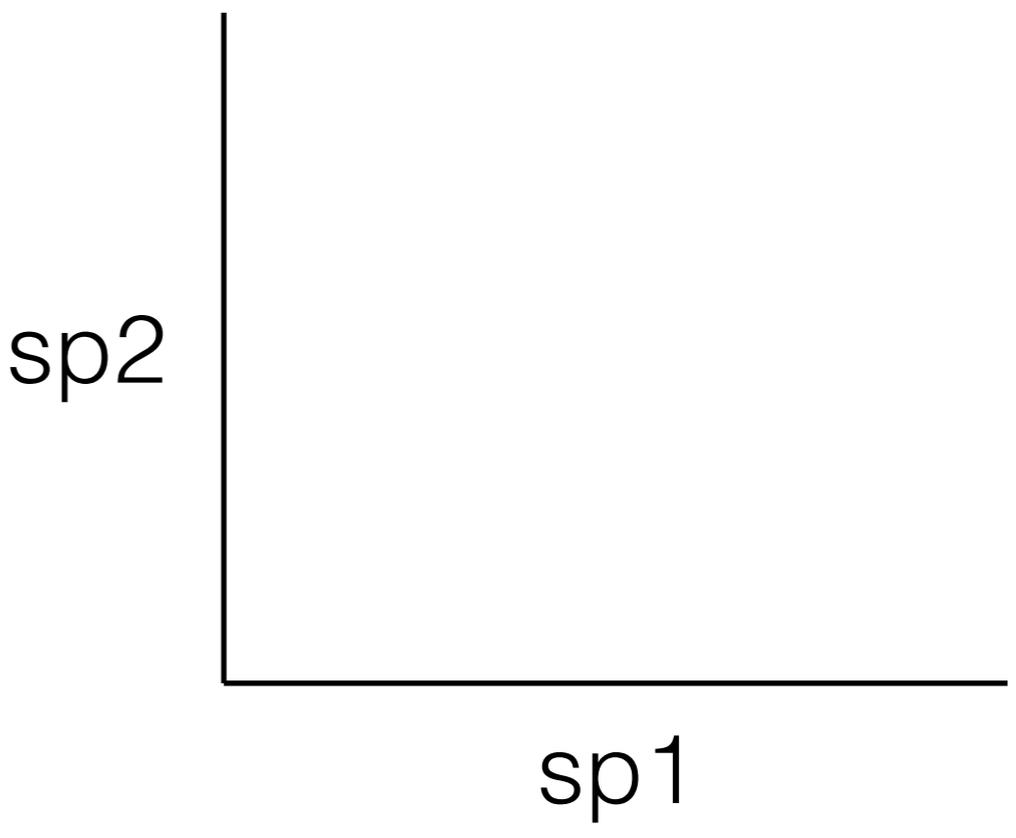
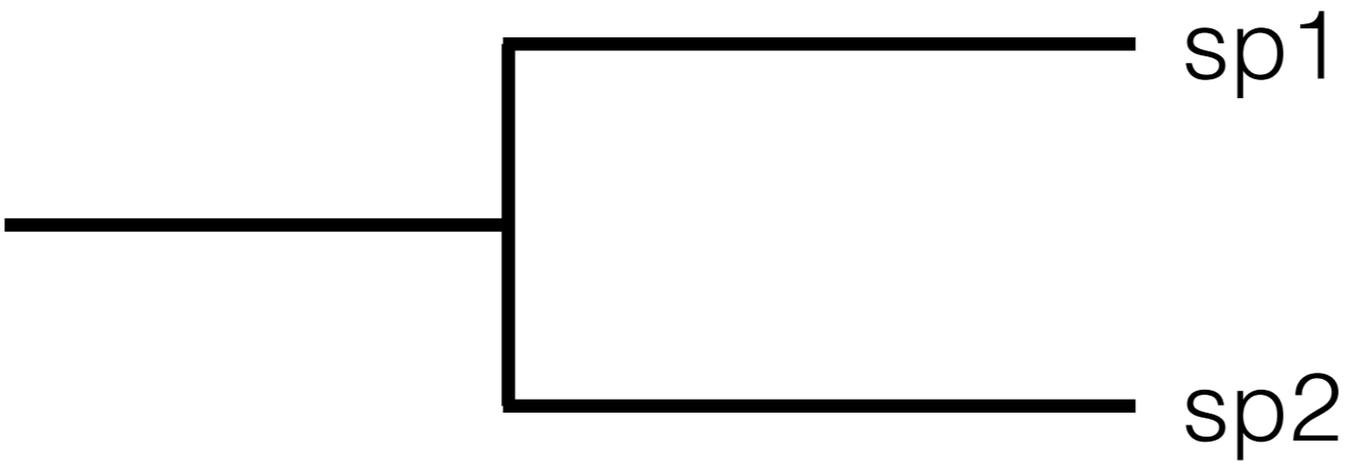


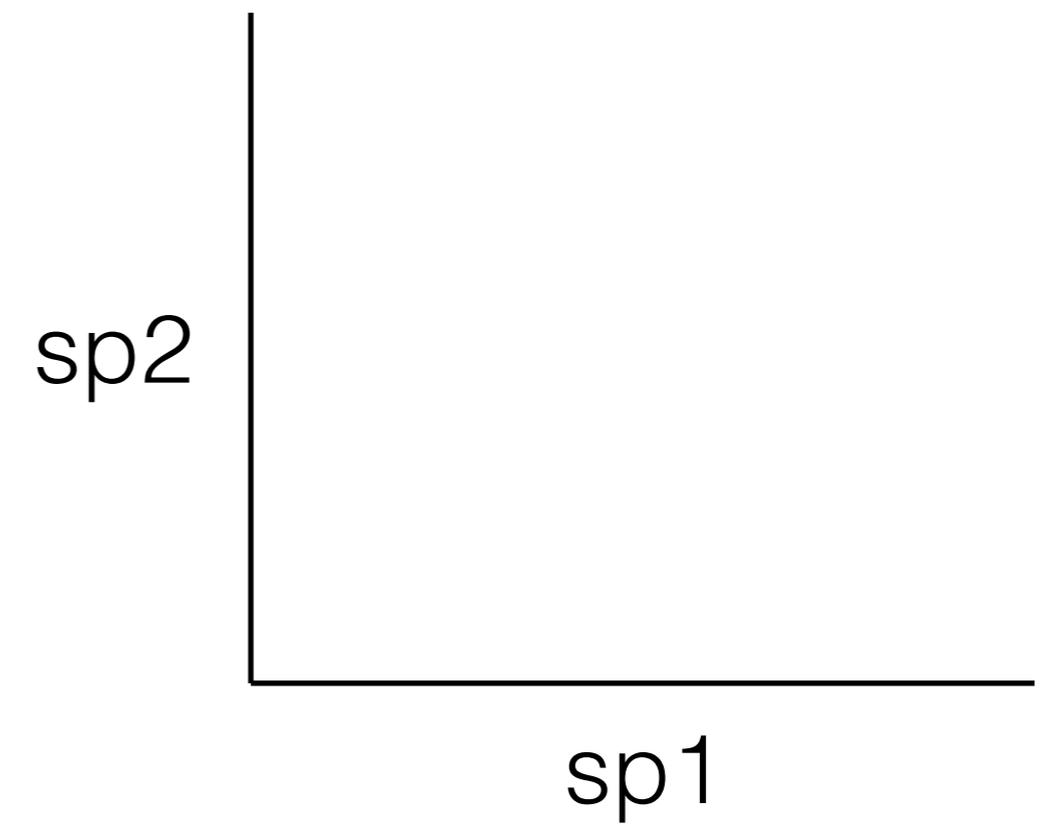
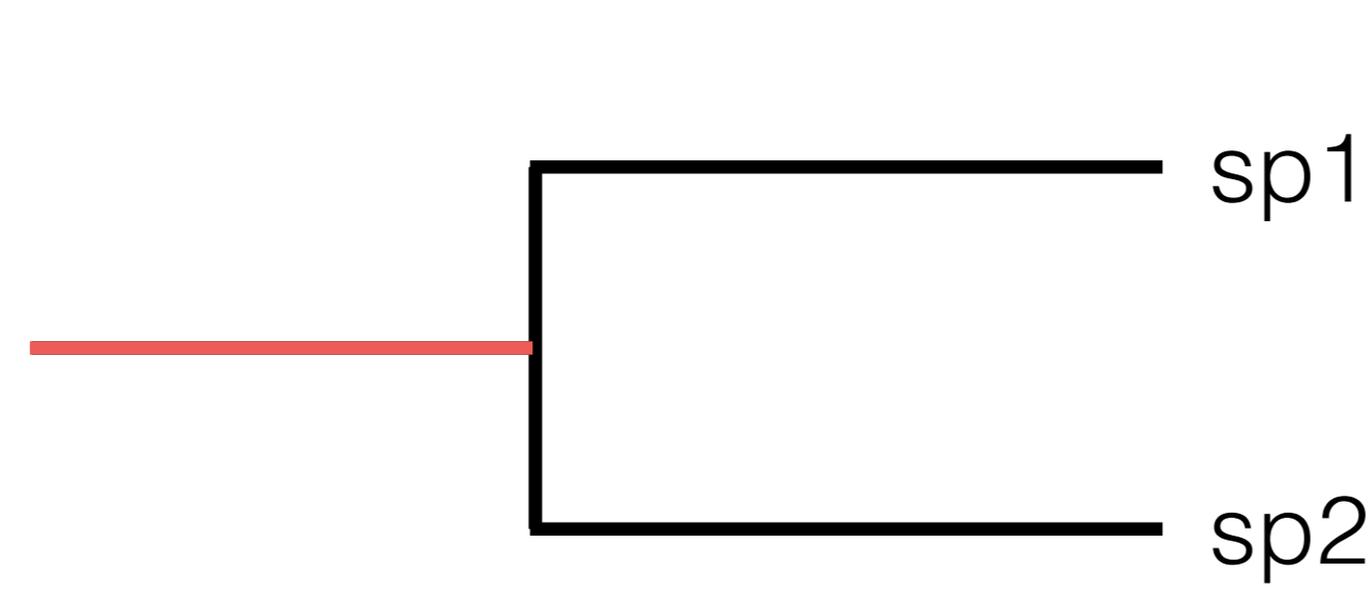
C_3 is contrast in values between (unobserved) species value of node 1 and (unobserved) species value of node 2

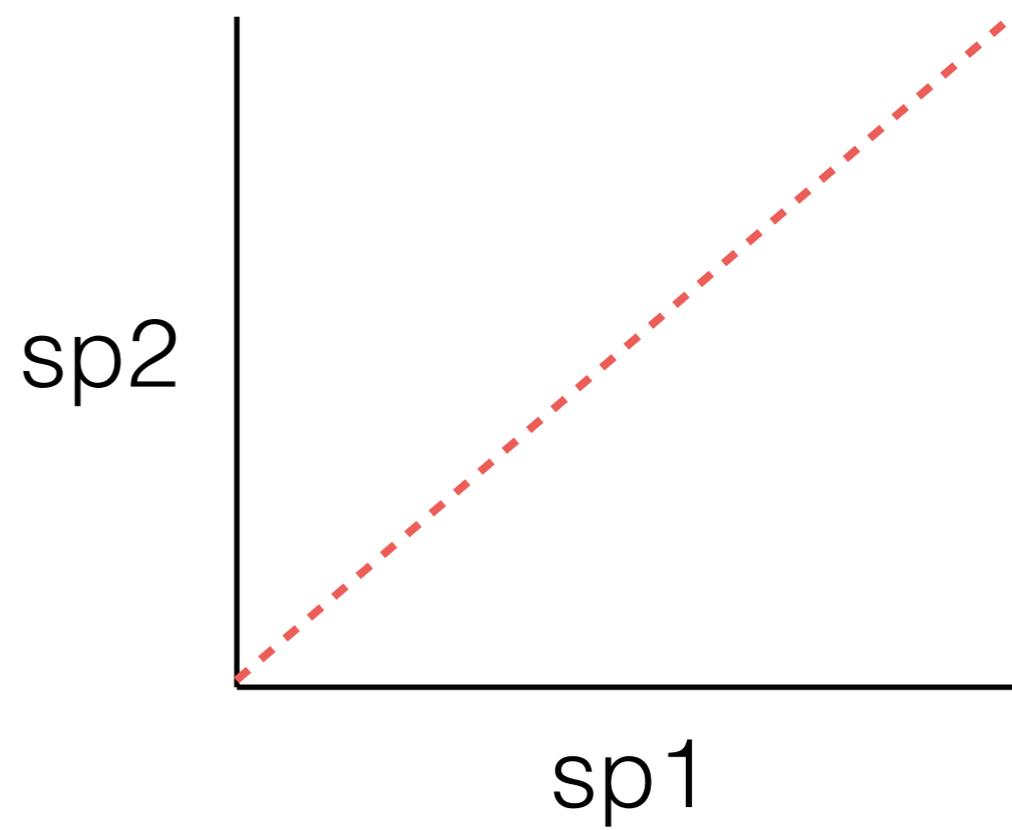
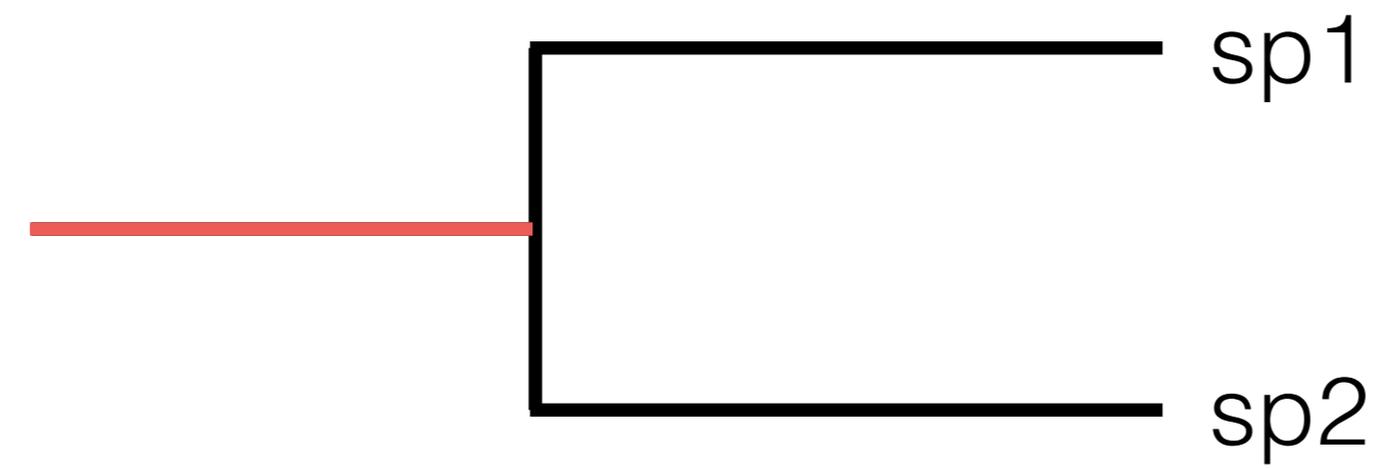
unobserved values can be estimated from their respective daughter species

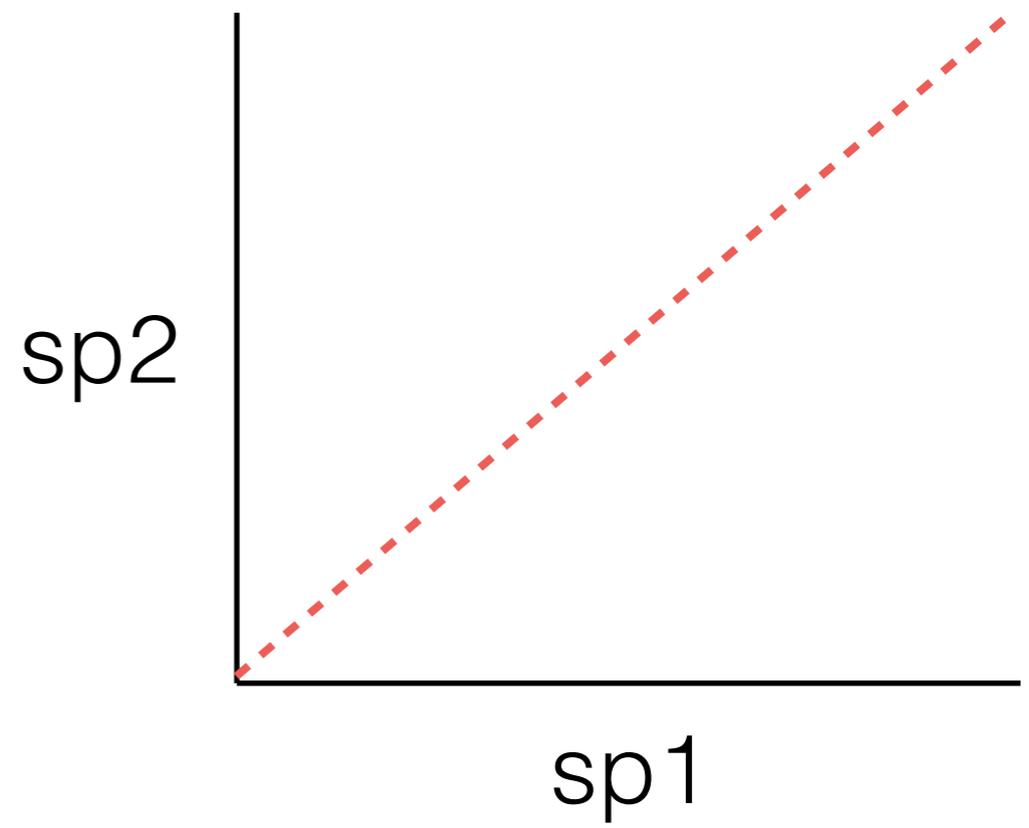
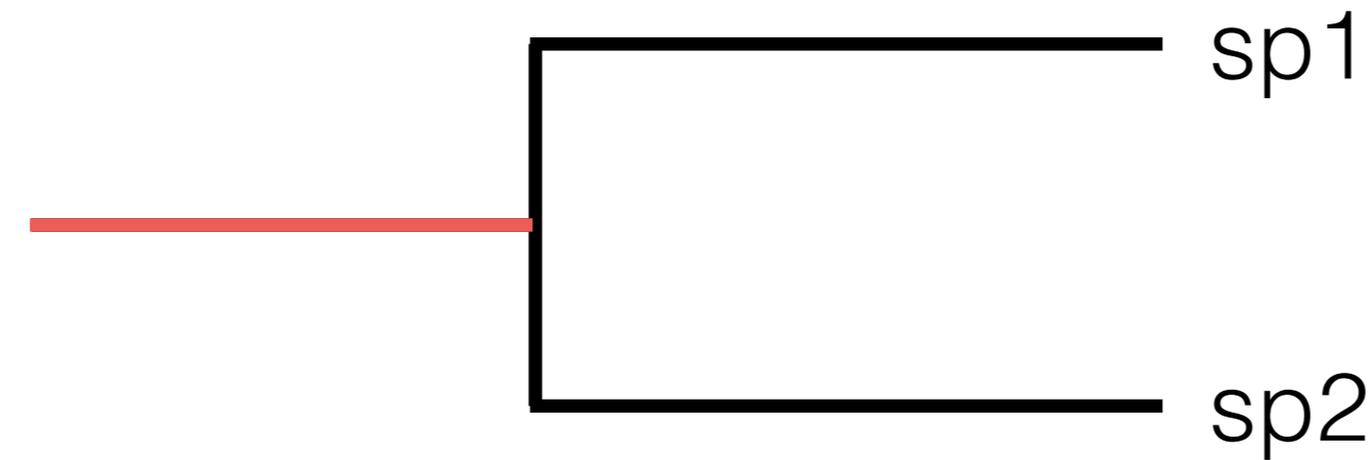


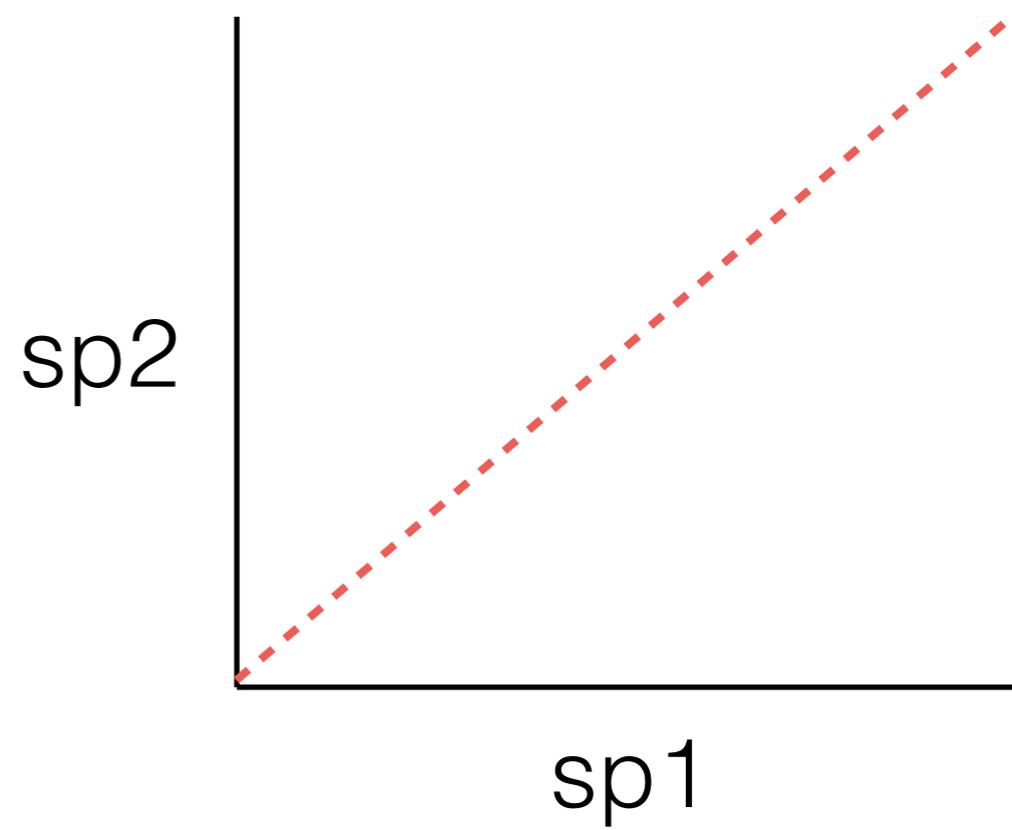
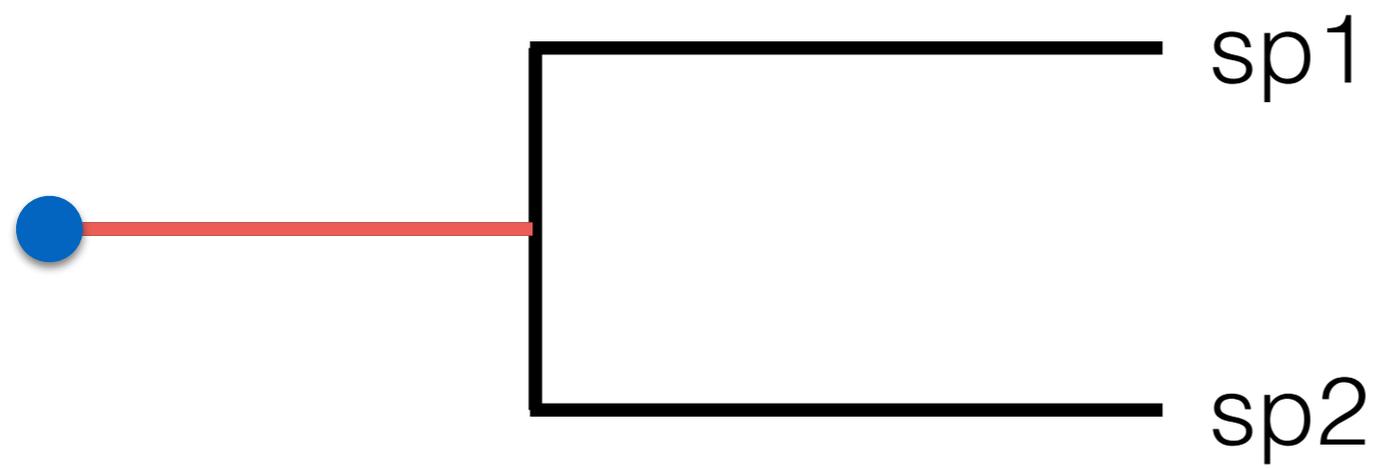


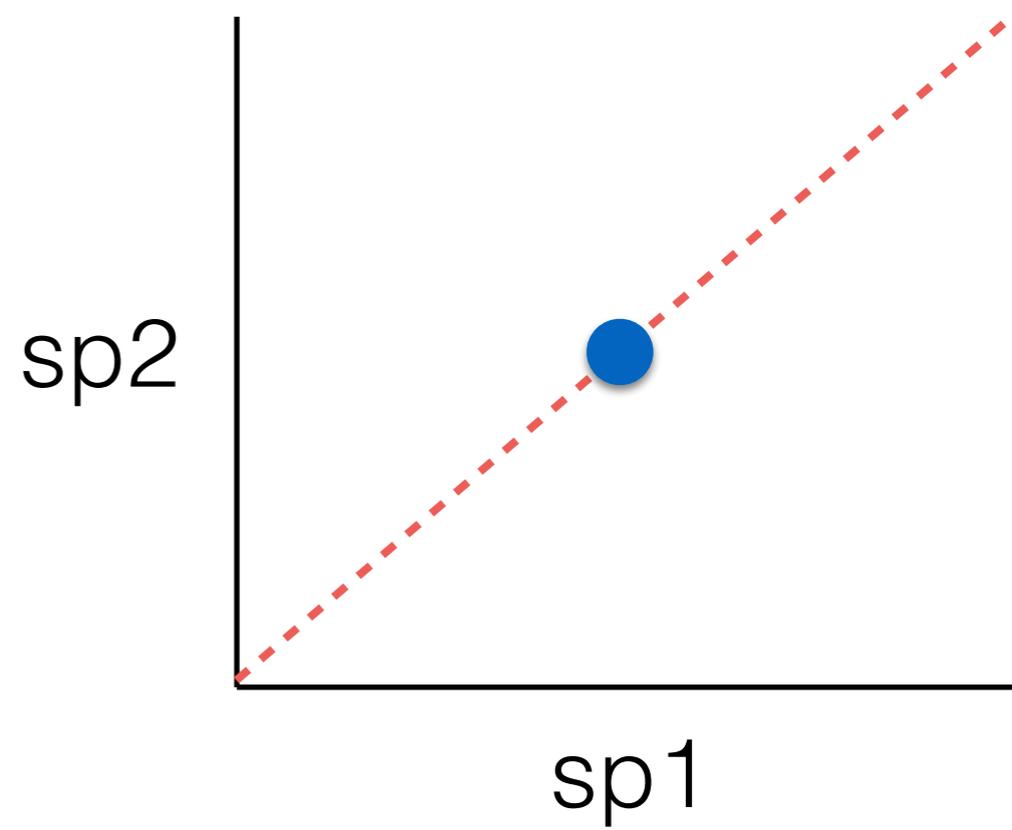
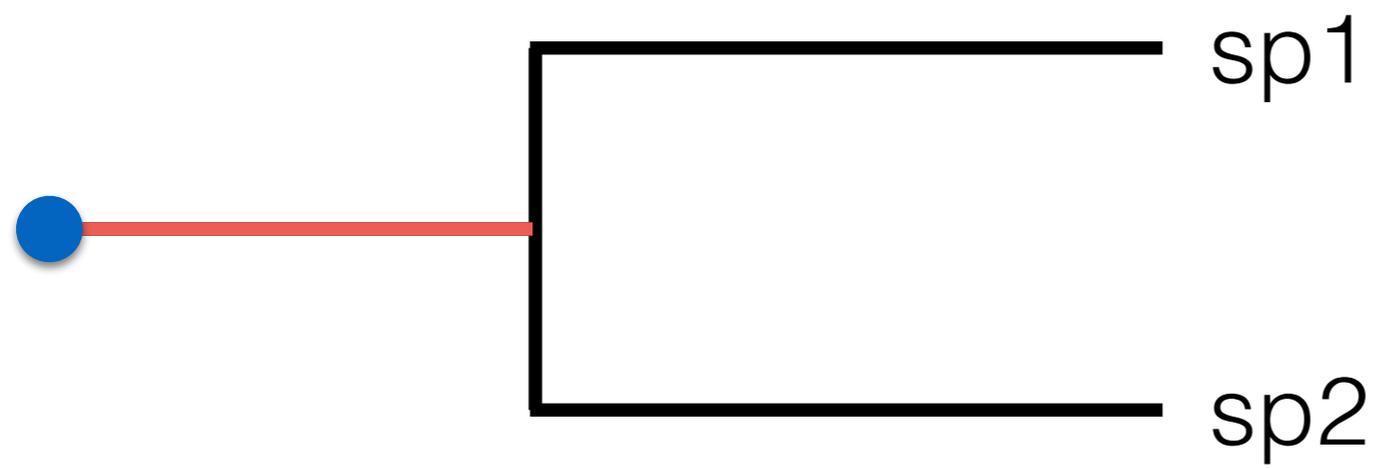


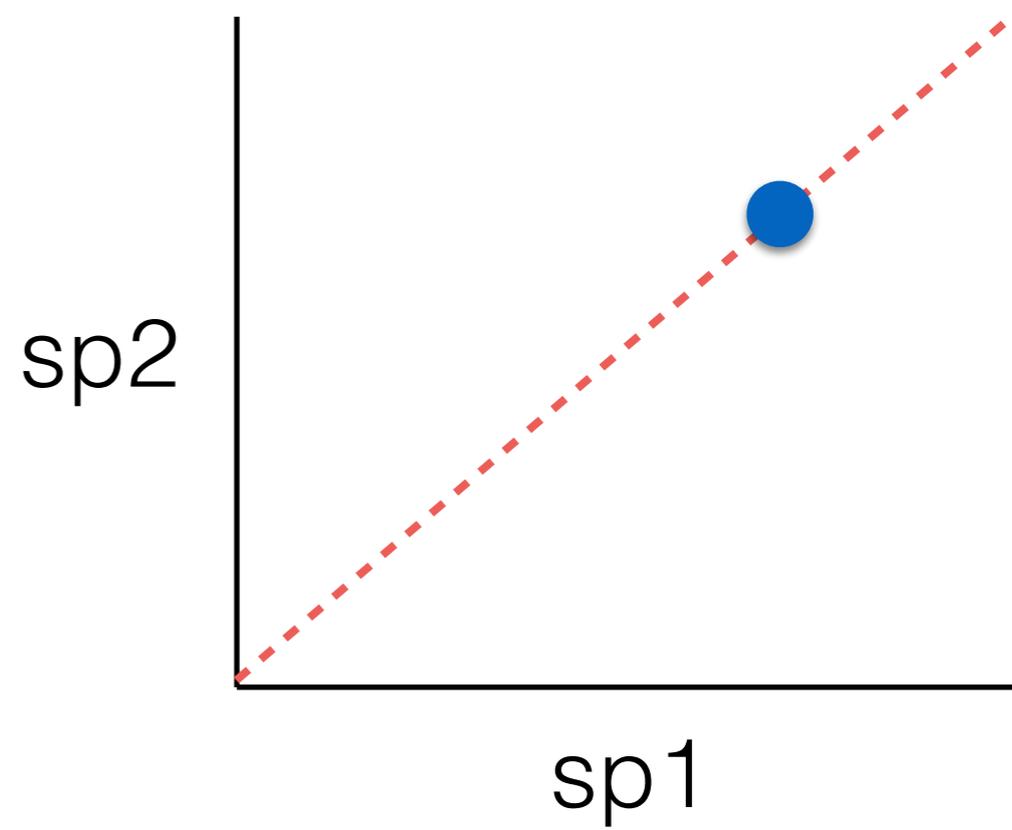
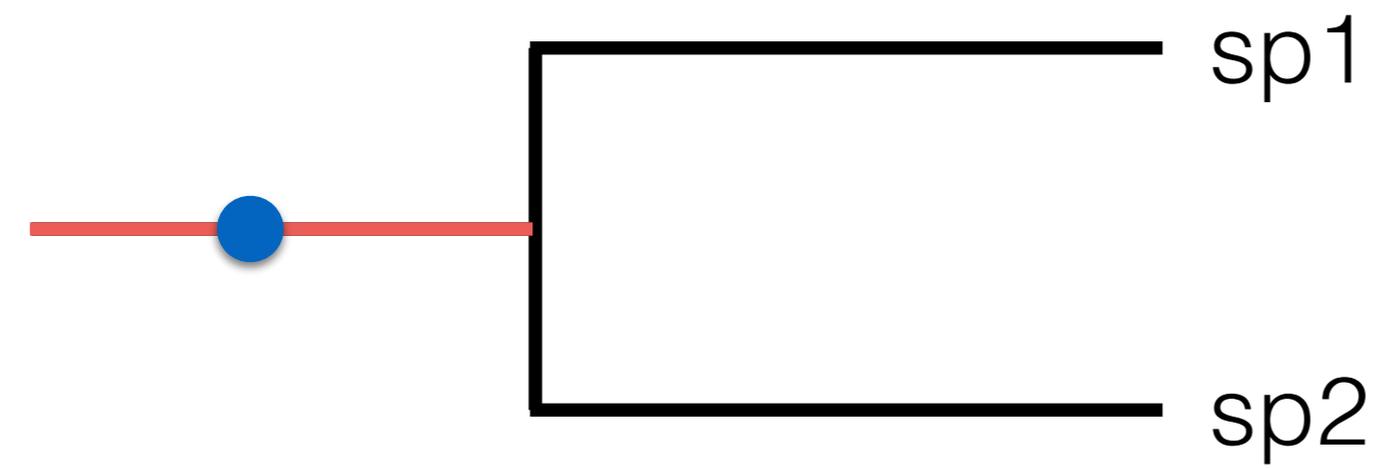


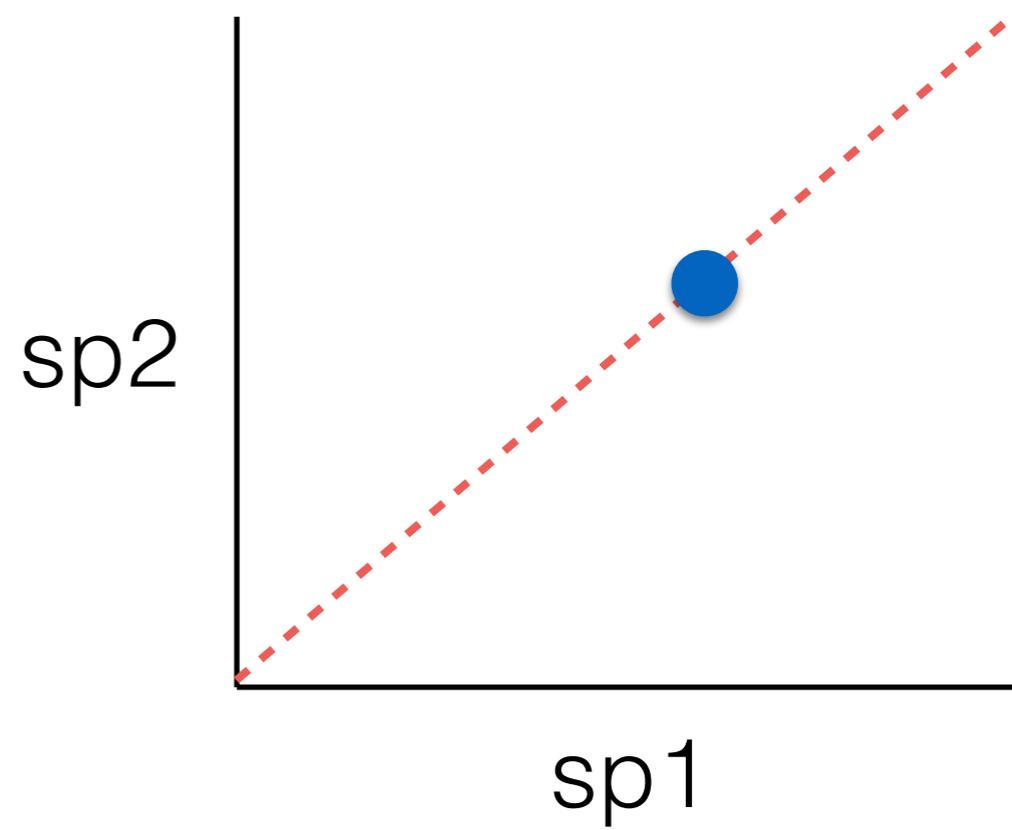
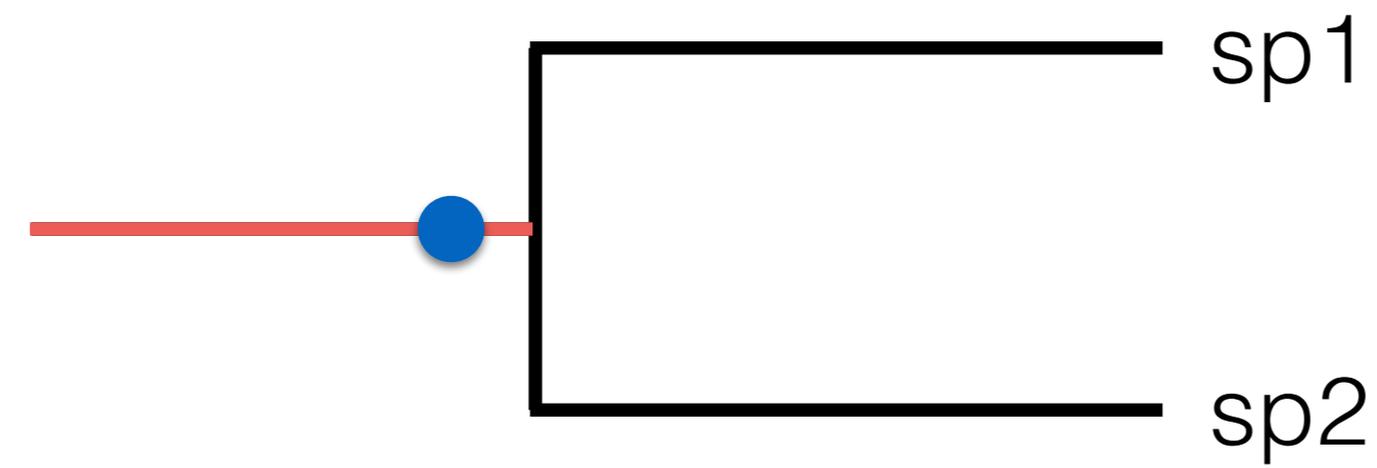


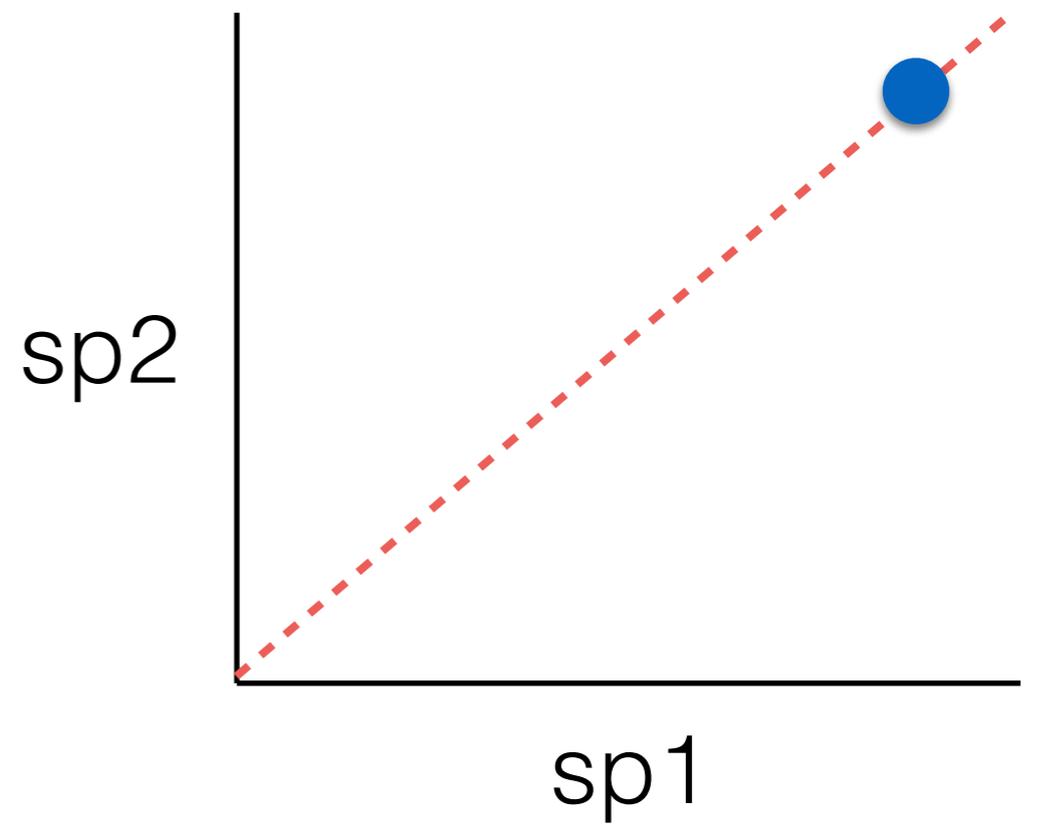
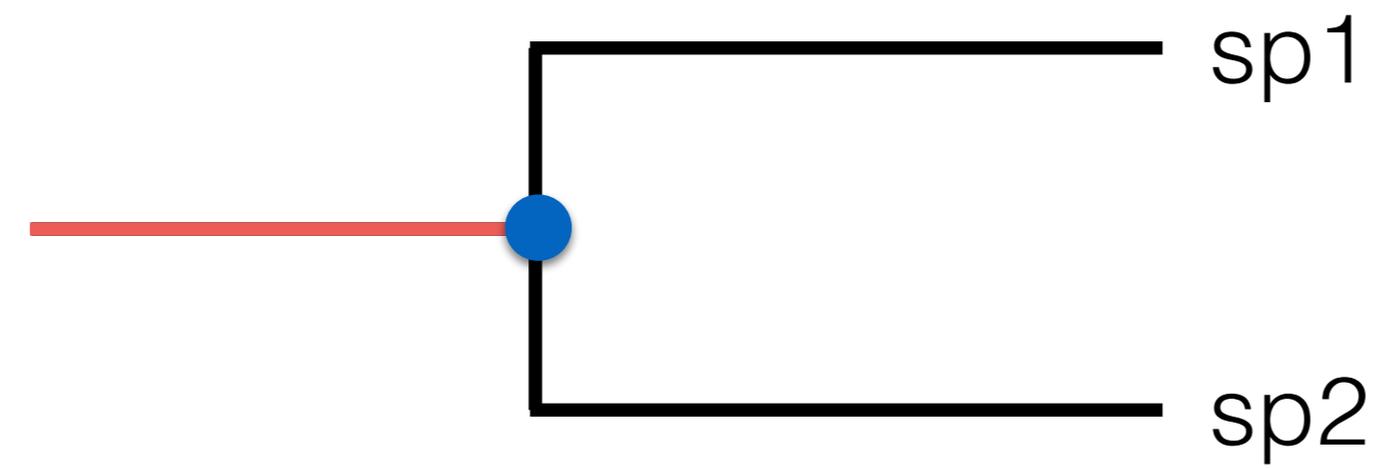


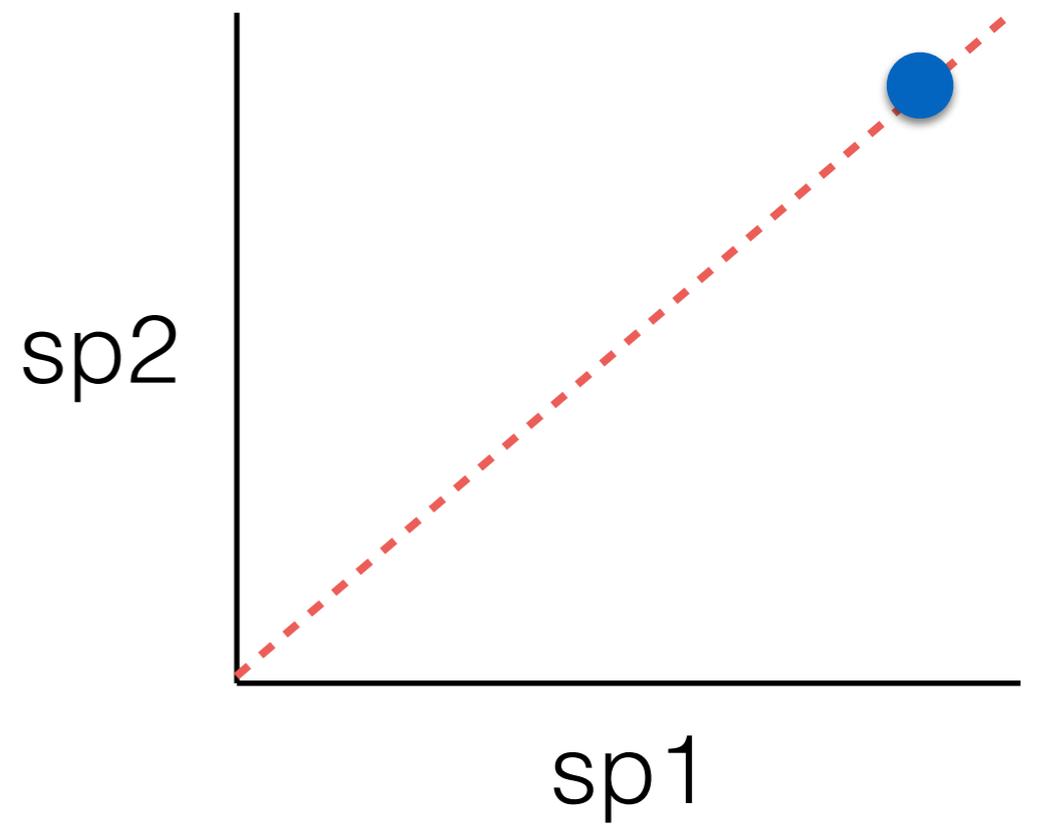
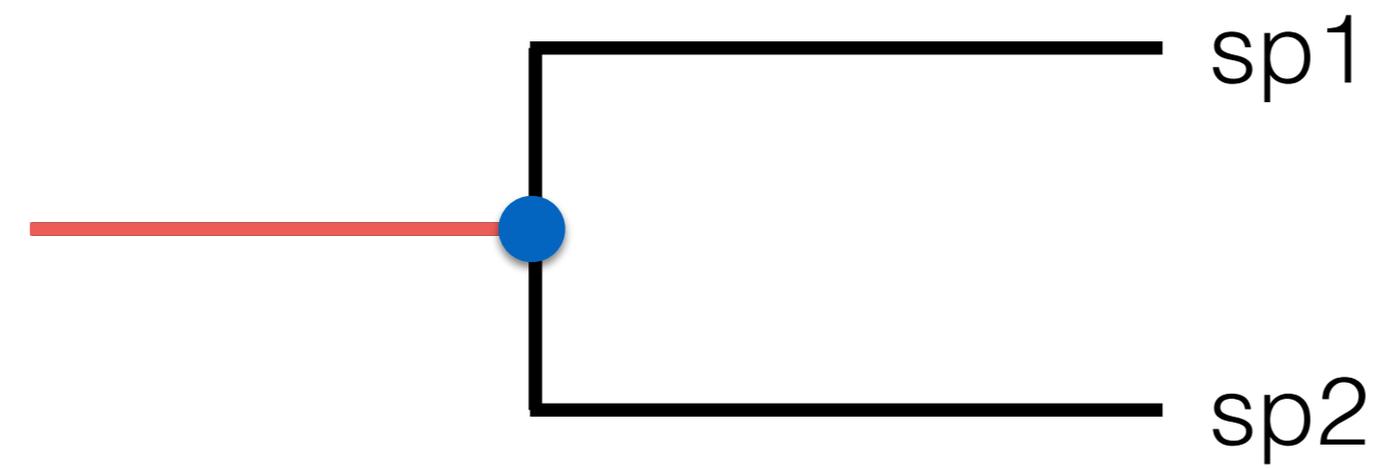


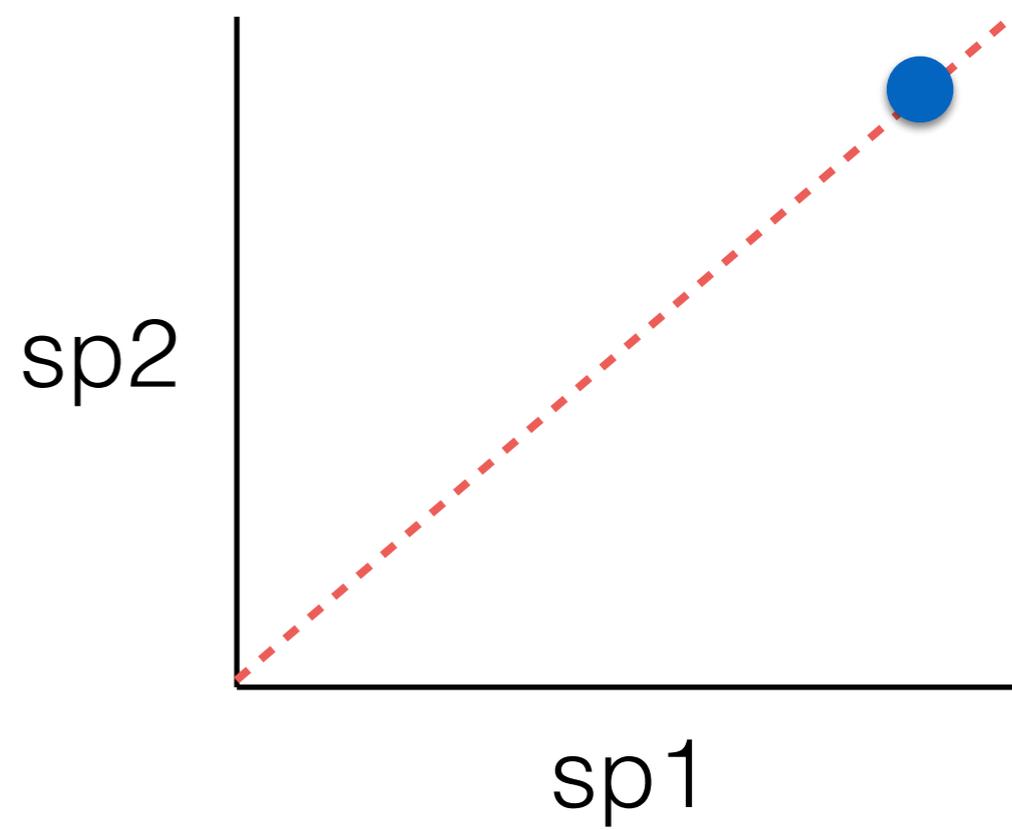
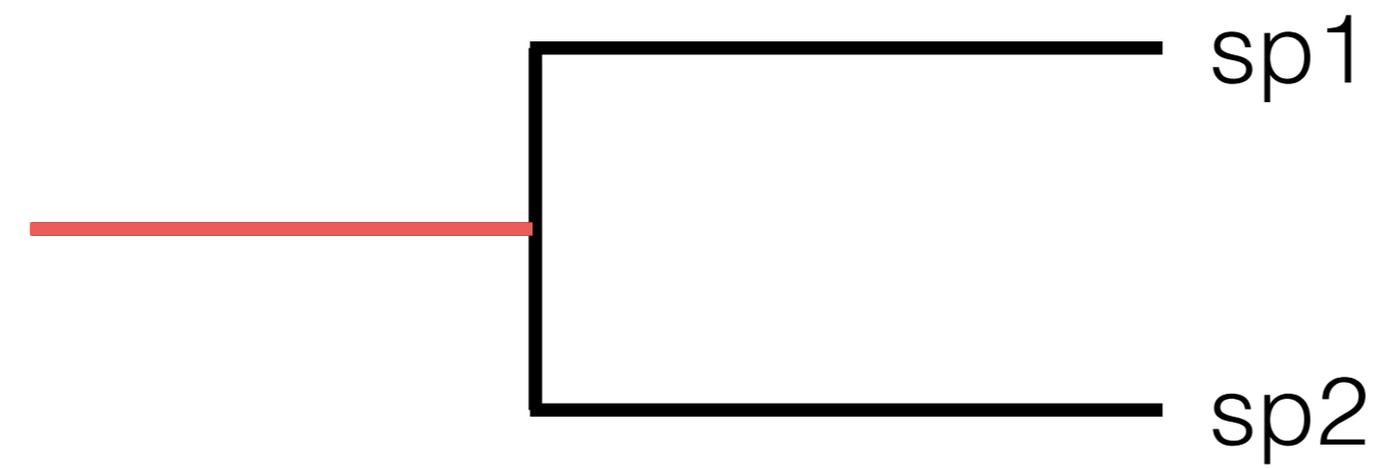


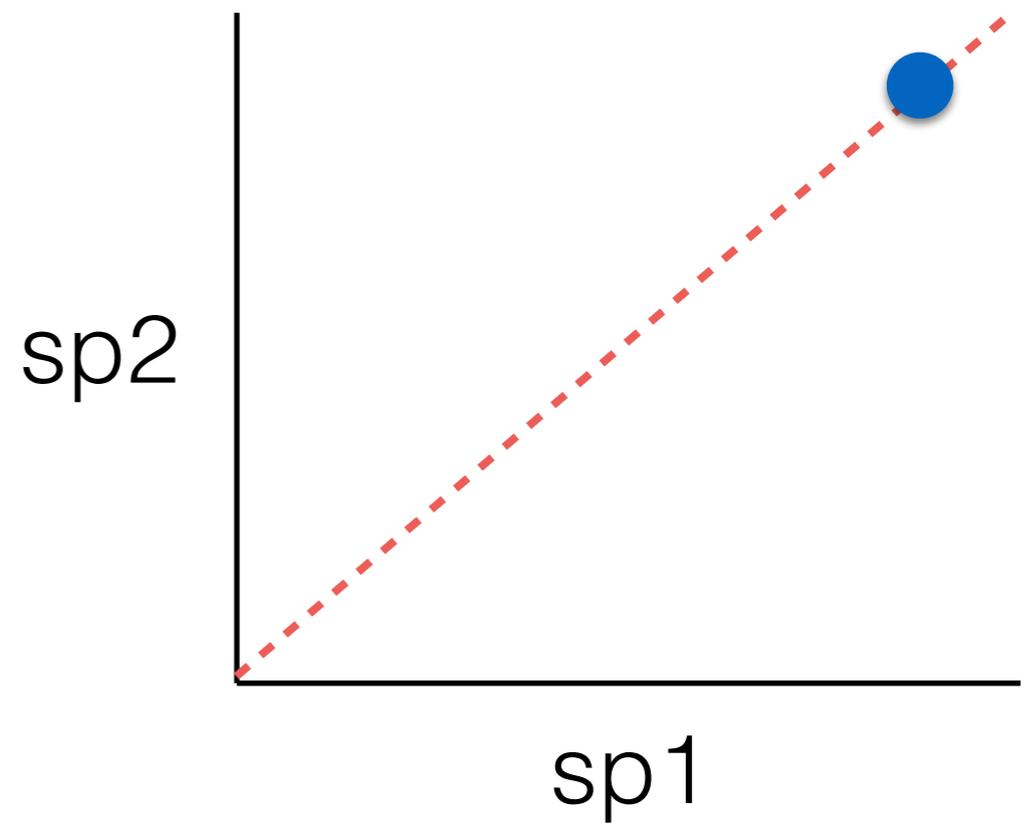
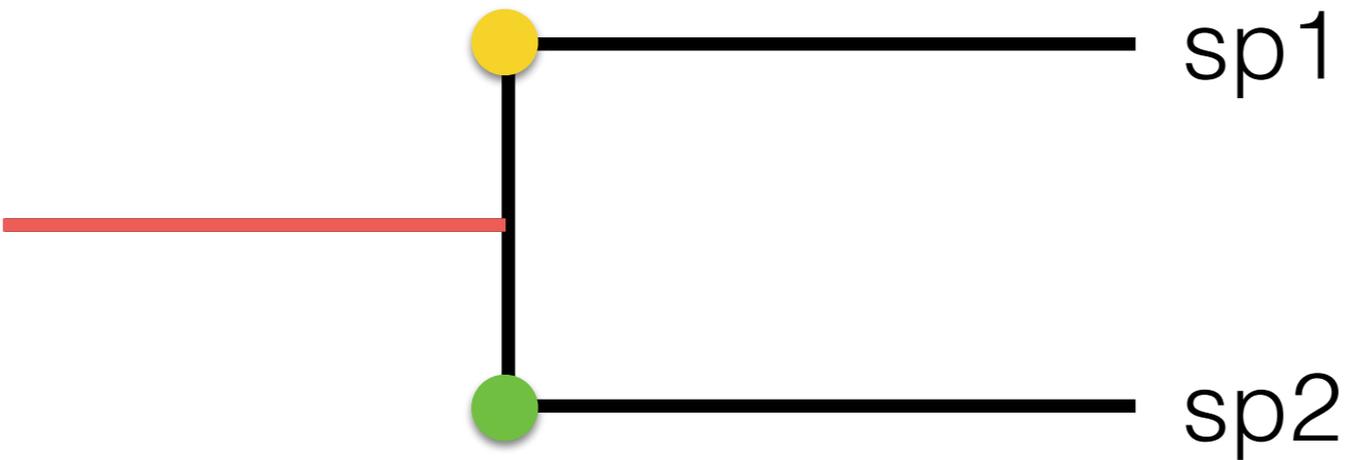


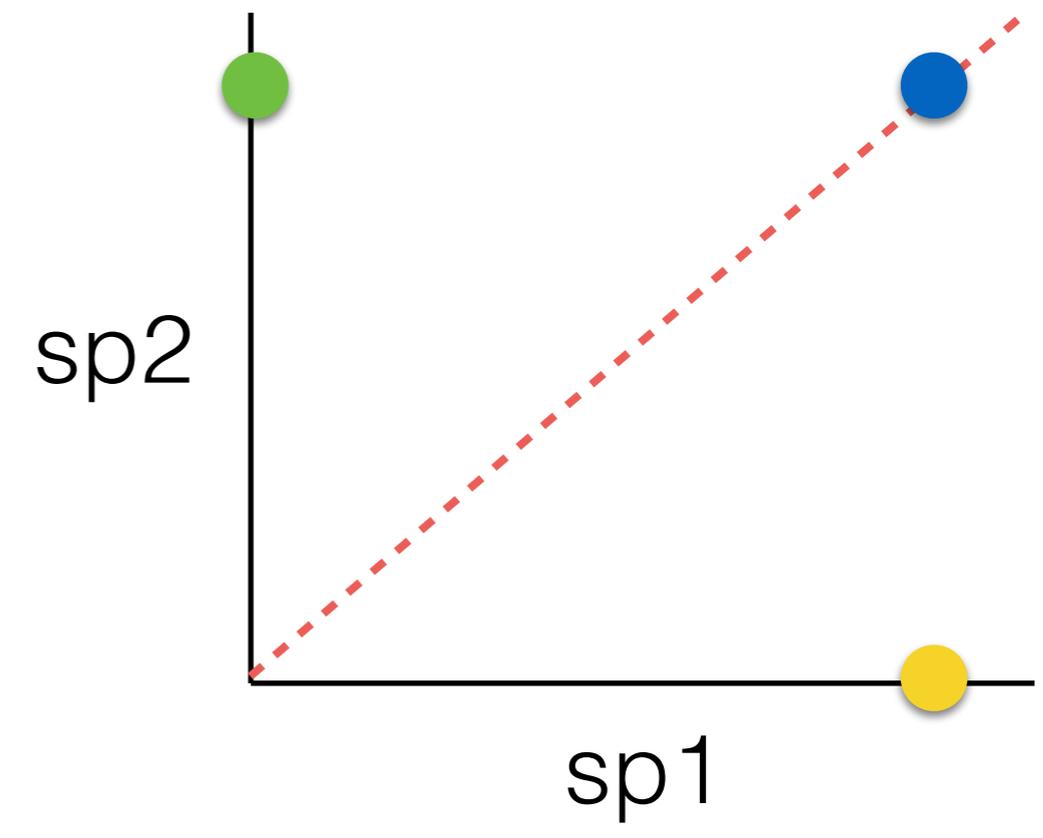
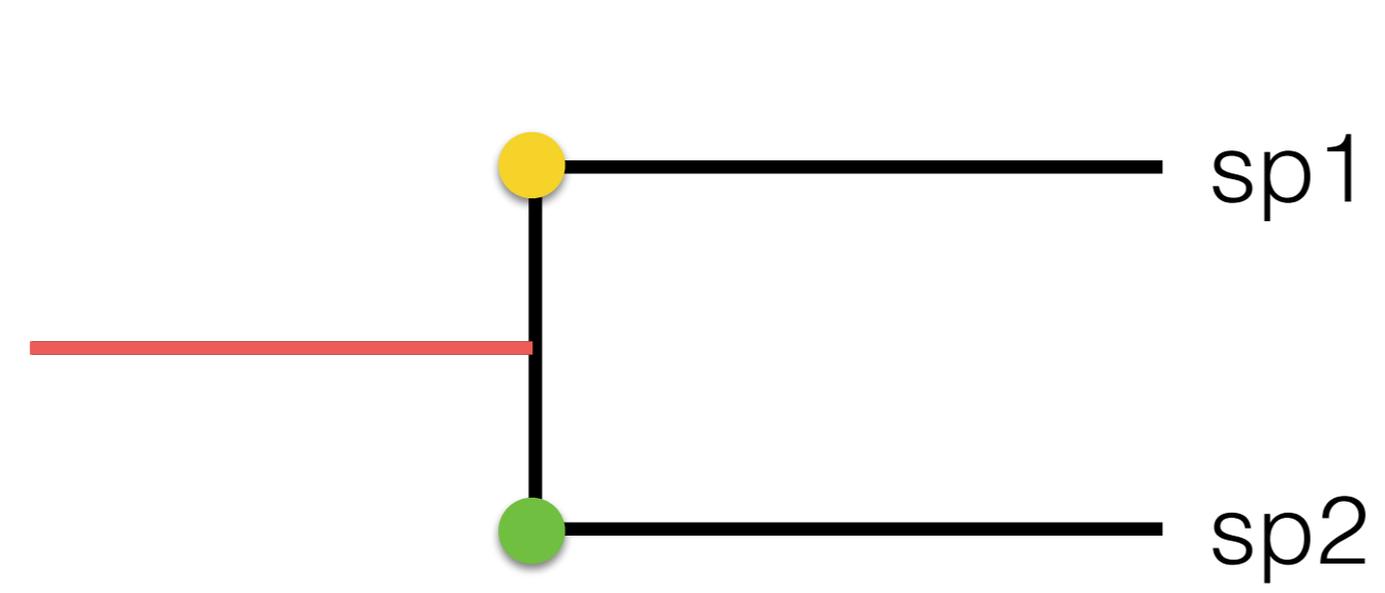


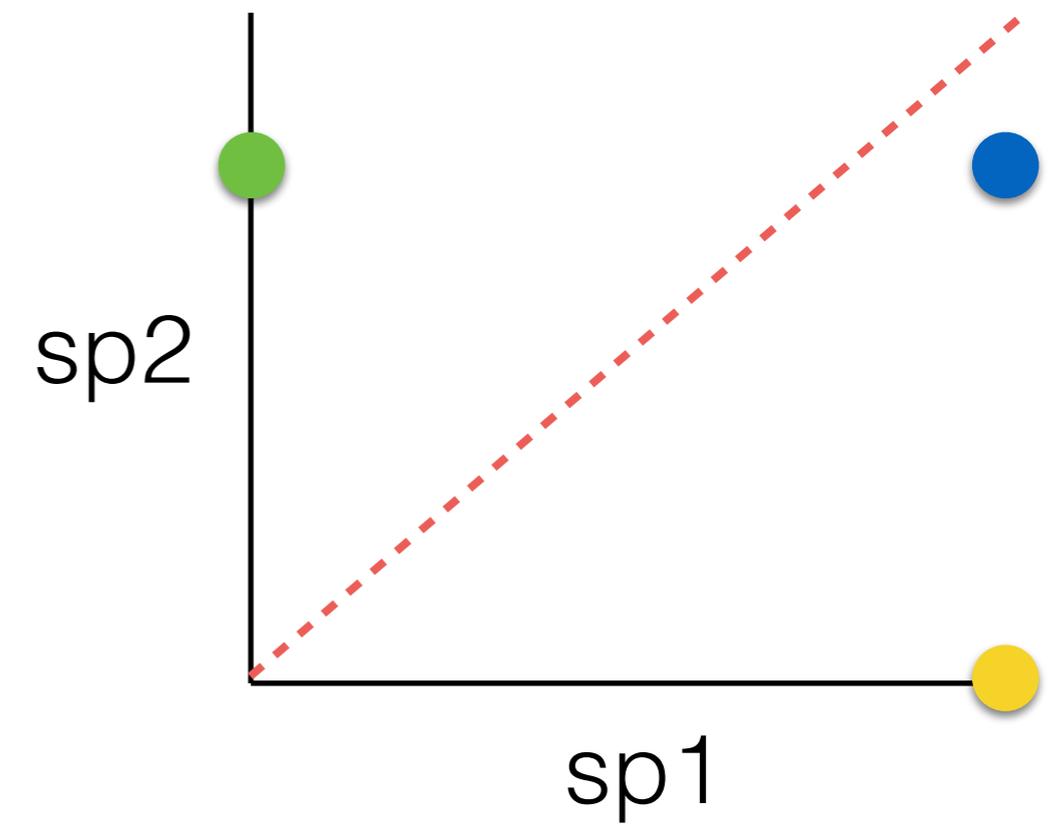
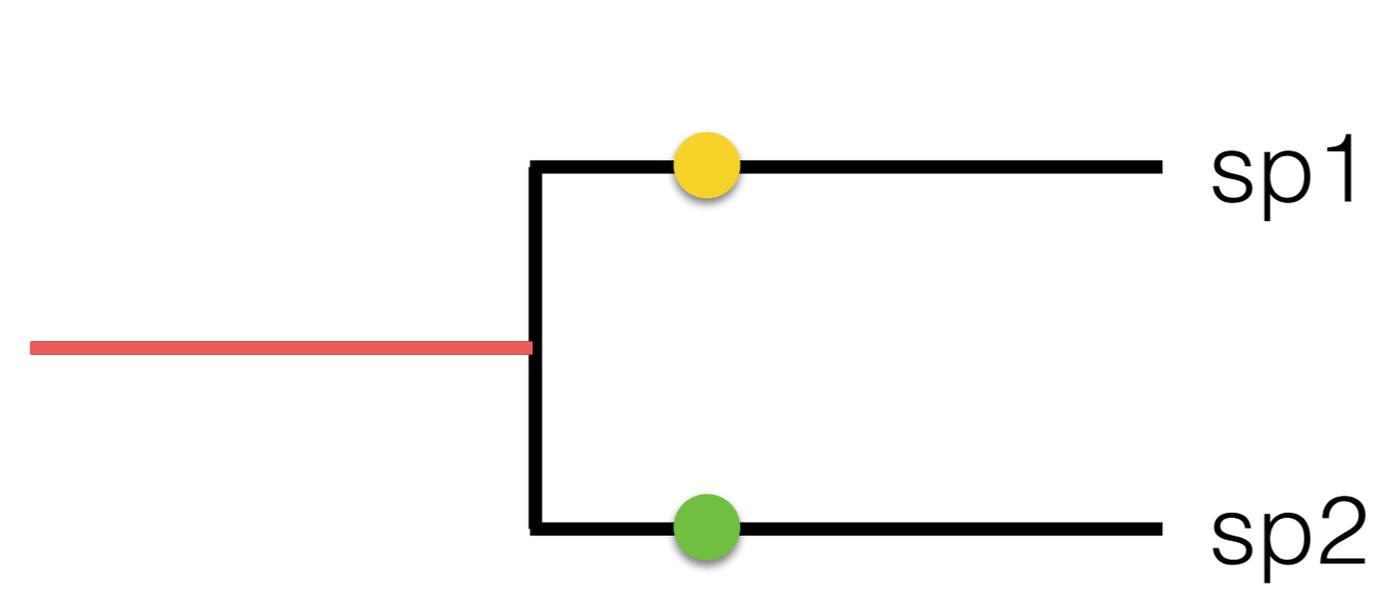


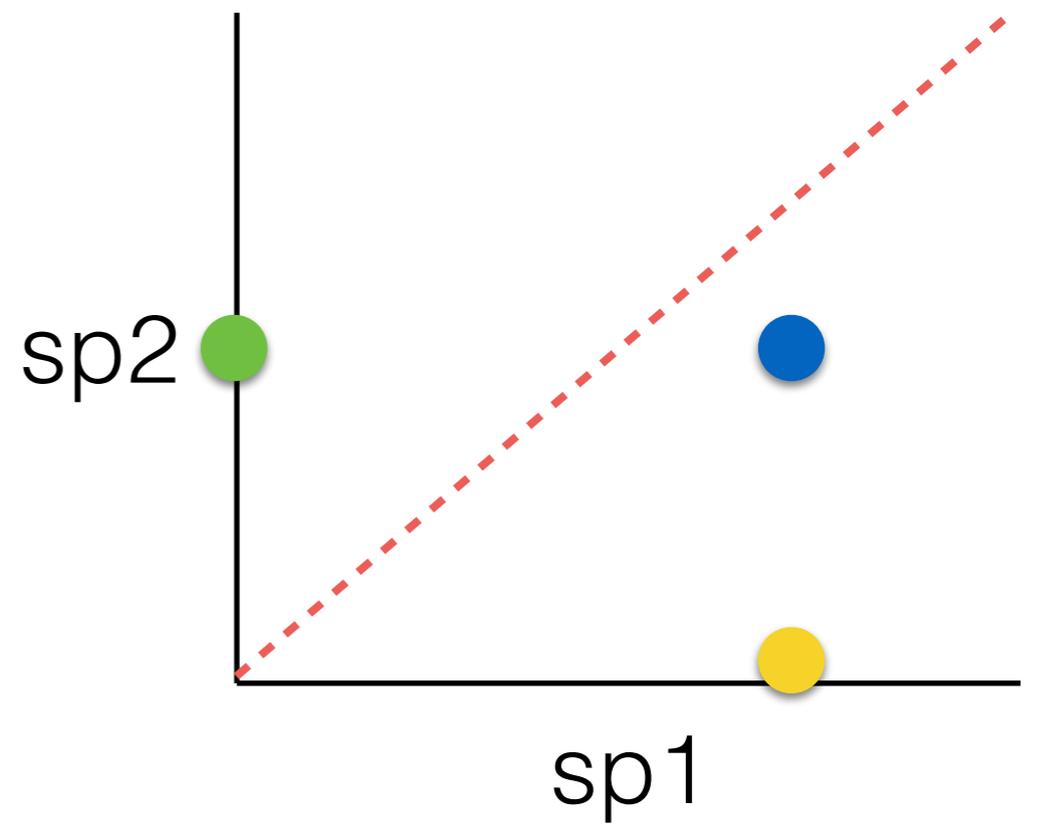
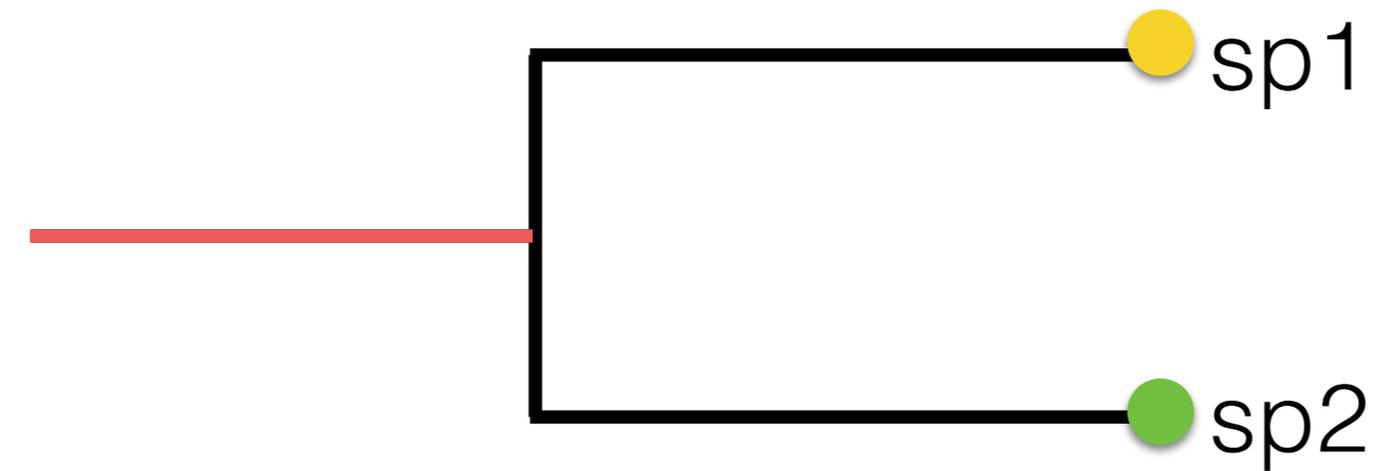


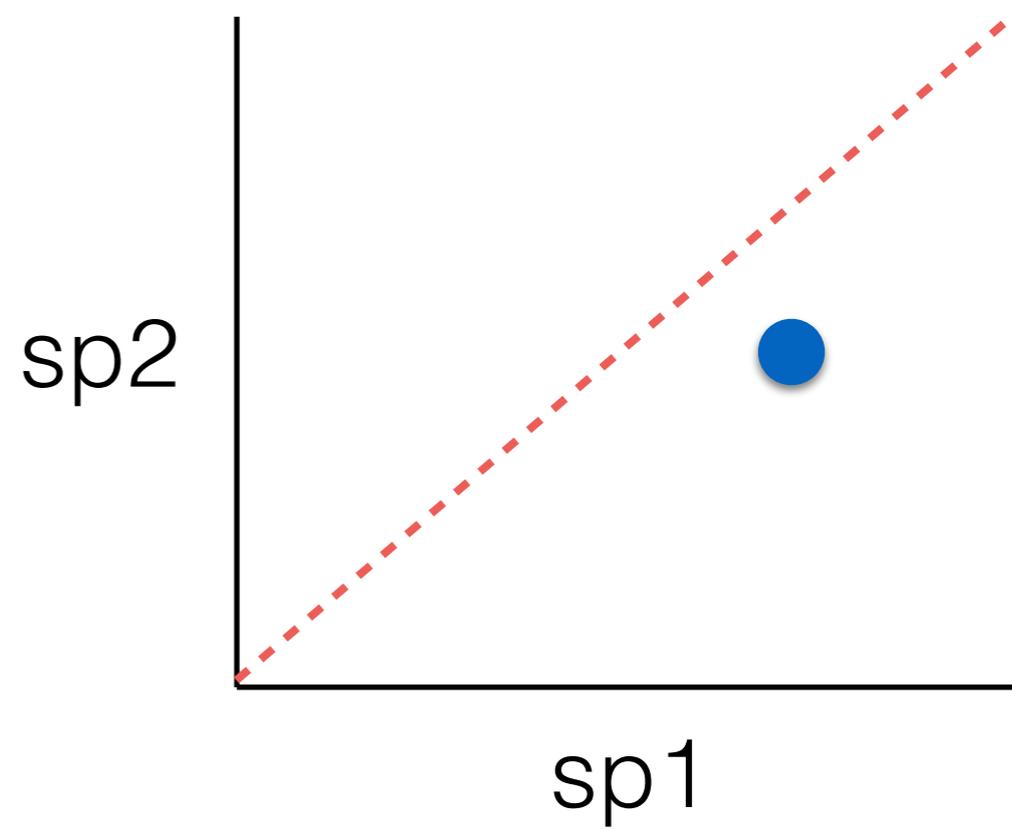
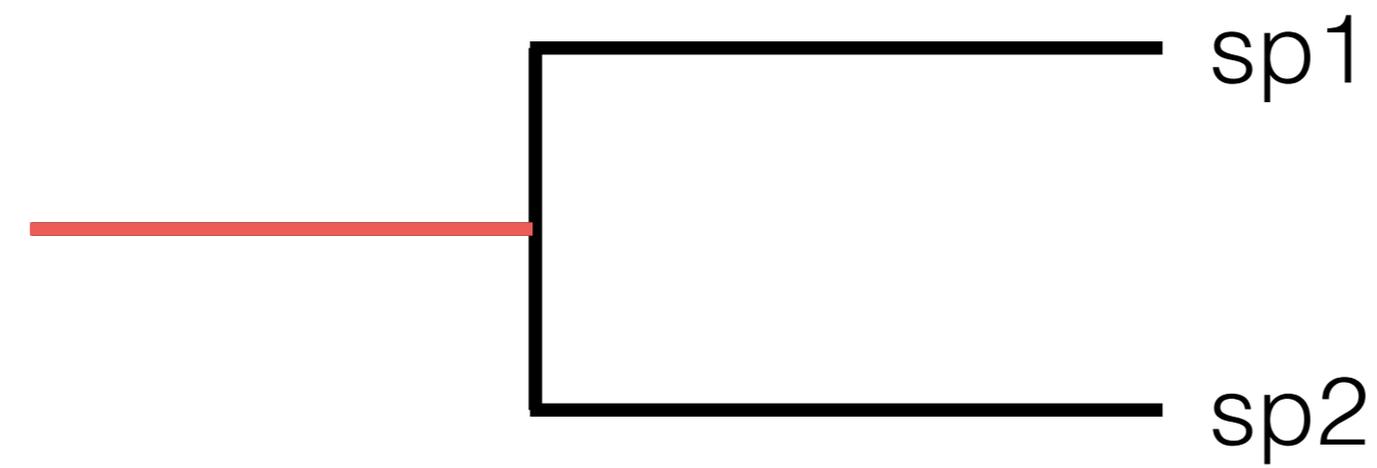






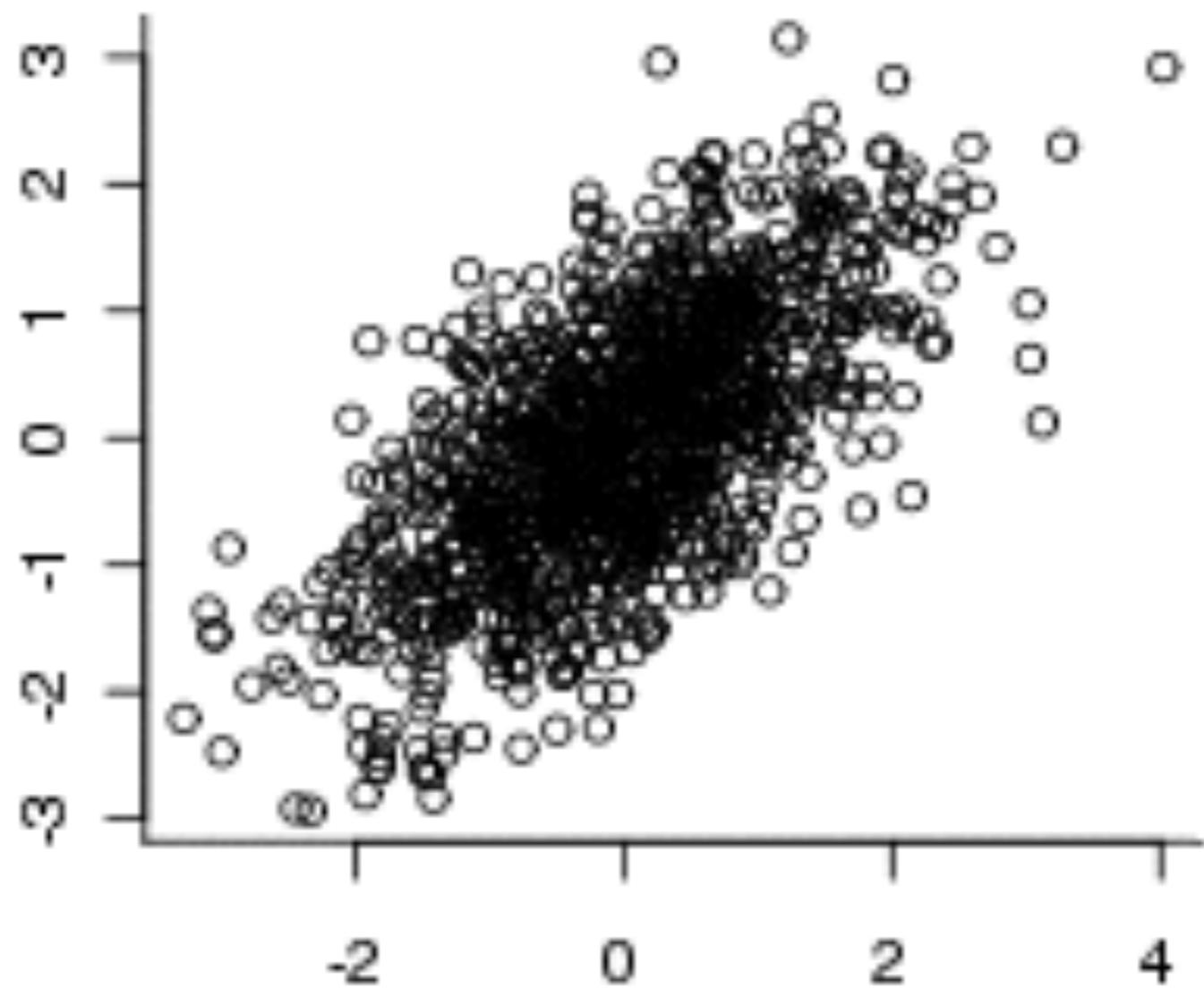






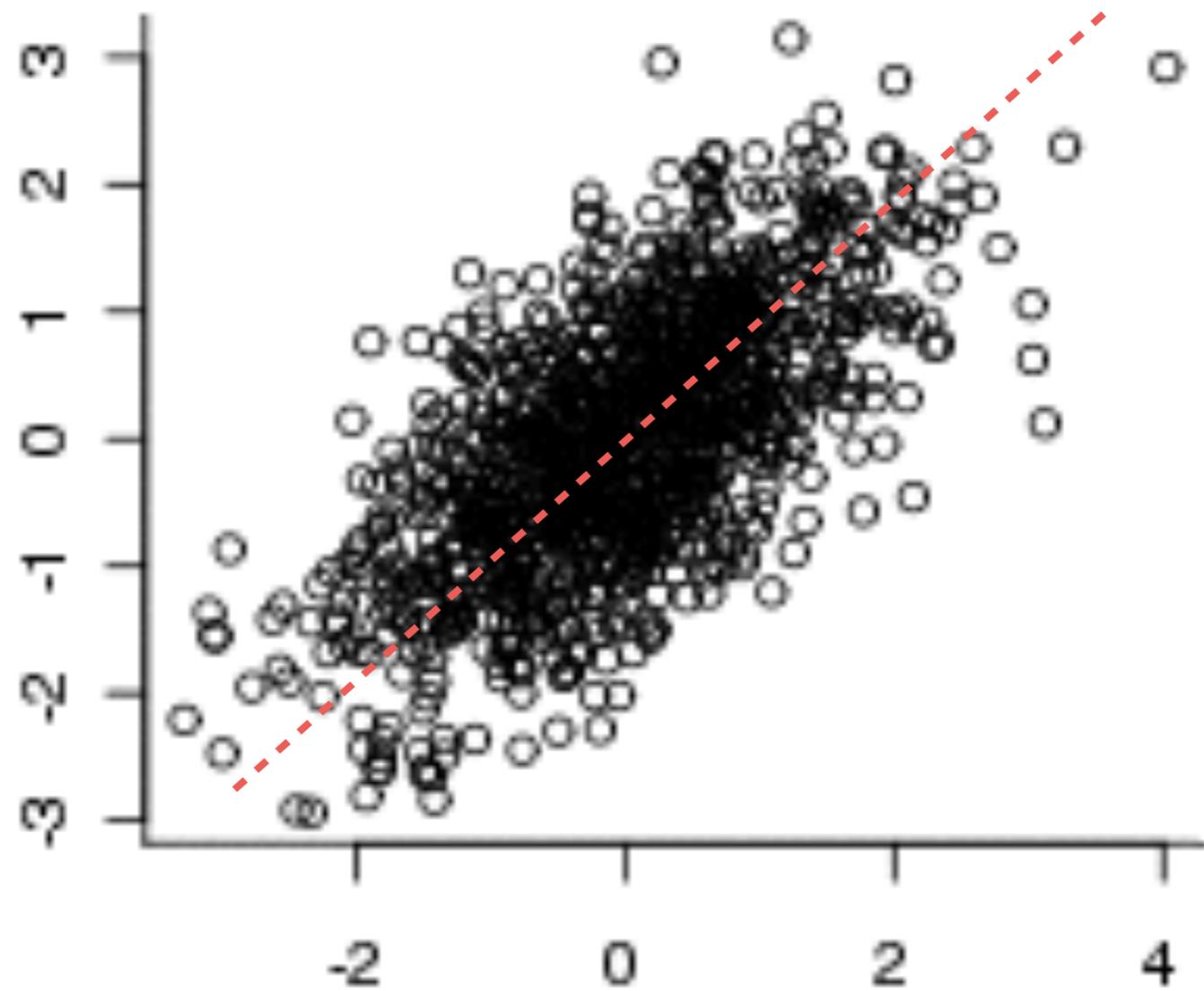
Species covary because they
descend from a common ancestor

sp2



sp1

sp2

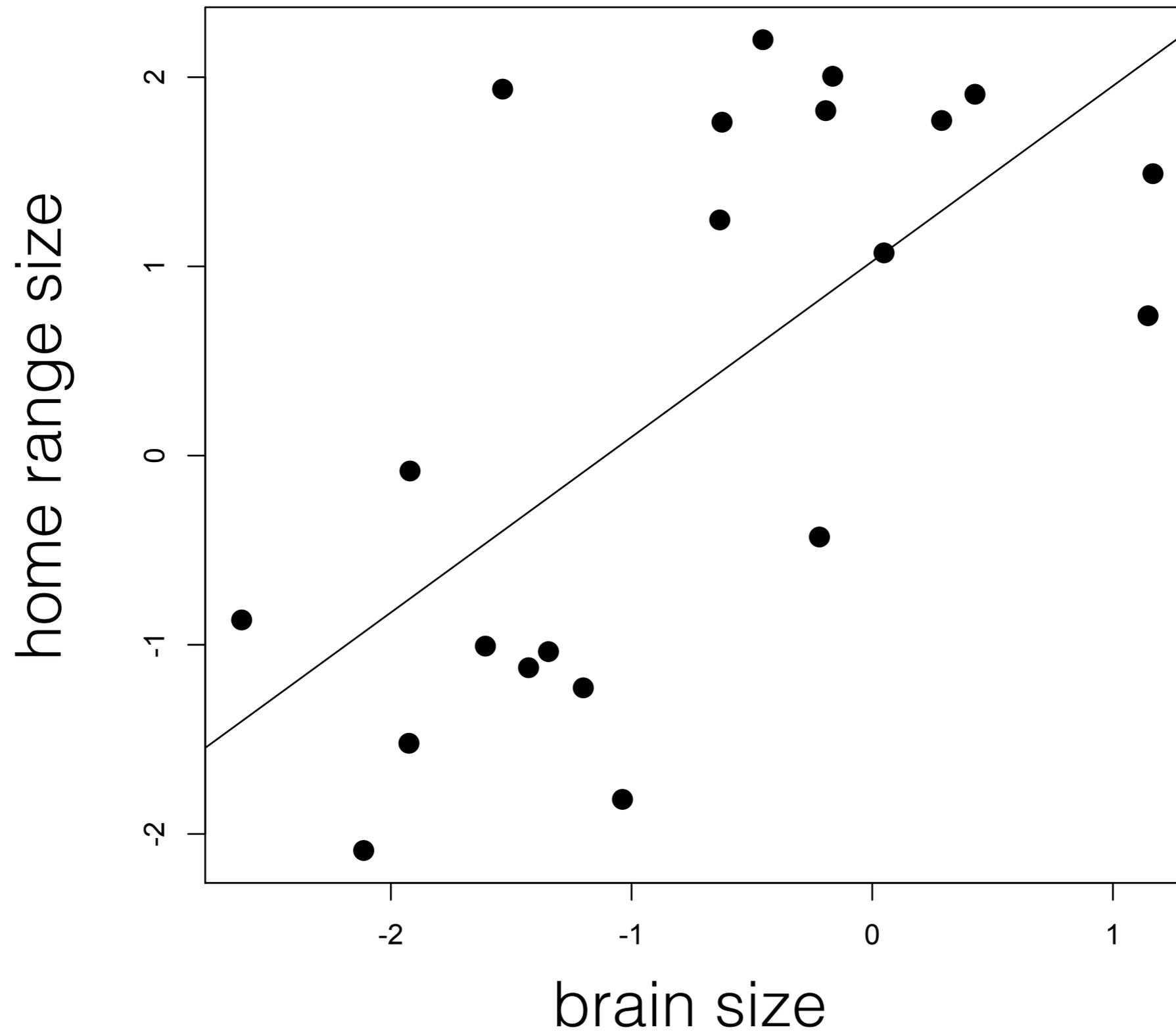


sp1

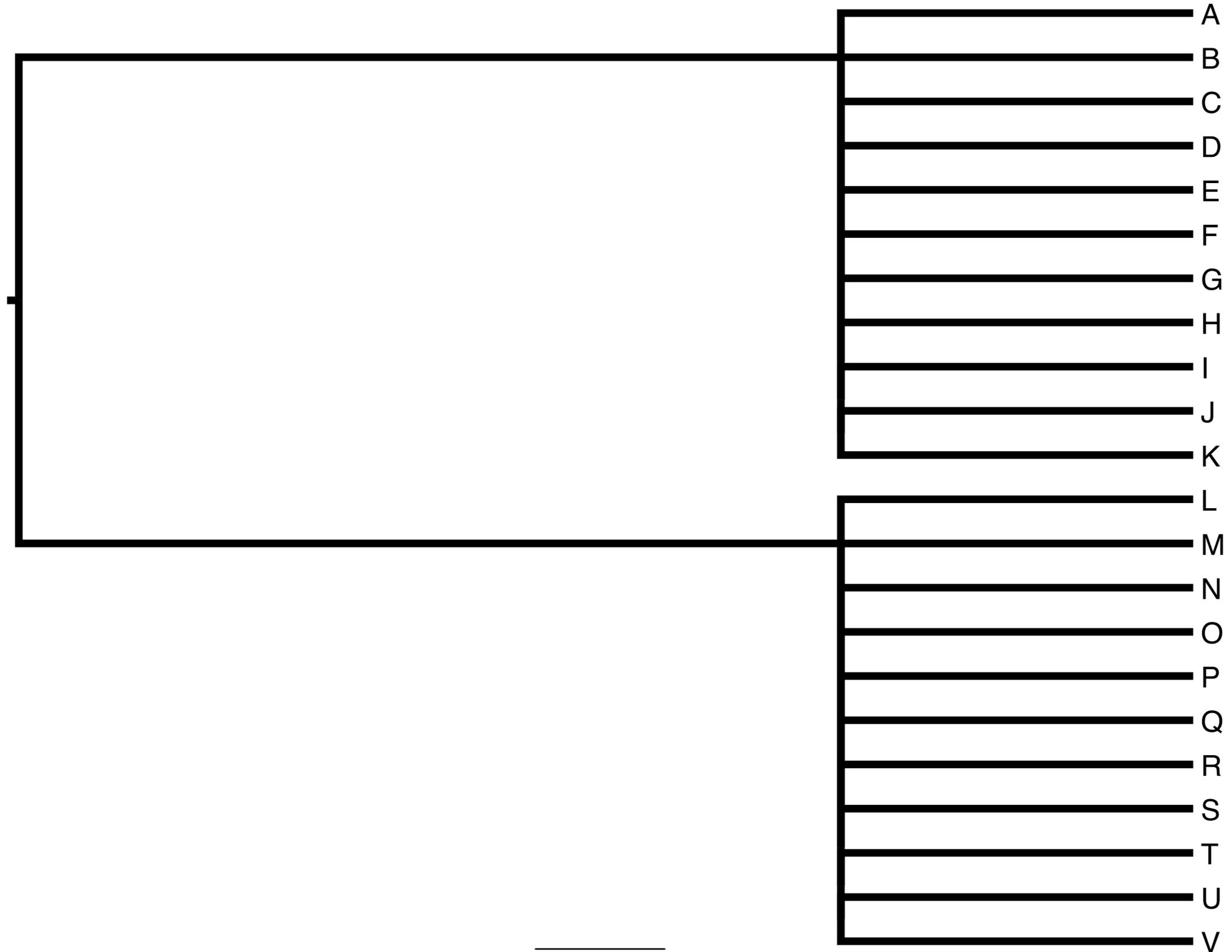
Phylogenetic non-independence

- any set of species in an analysis will share an evolutionary history
- we expect closely related species to be more similar to each other than more distantly related species
- treating species as independent in statistical analyses can be misleading

do species with bigger brains have larger home ranges?



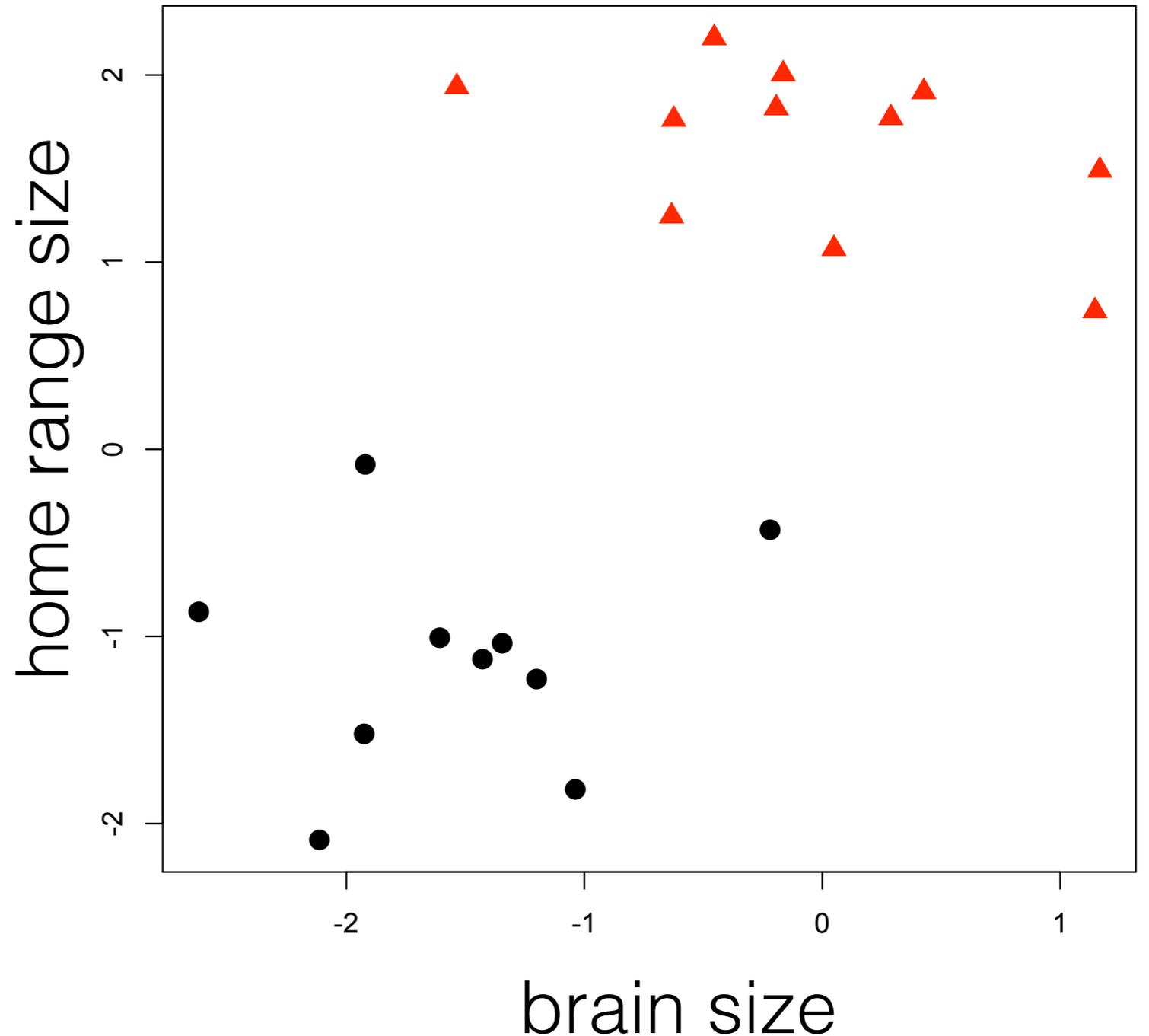
what if the phylogeny looks like this?



0.11

Need to account for phylogeny

- effectively have closer to two independent points, instead of 20
- are brain size and range size related?



Independent contrasts is a procedure for accounting for phylogenetic relatedness when making interspecific trait comparisons

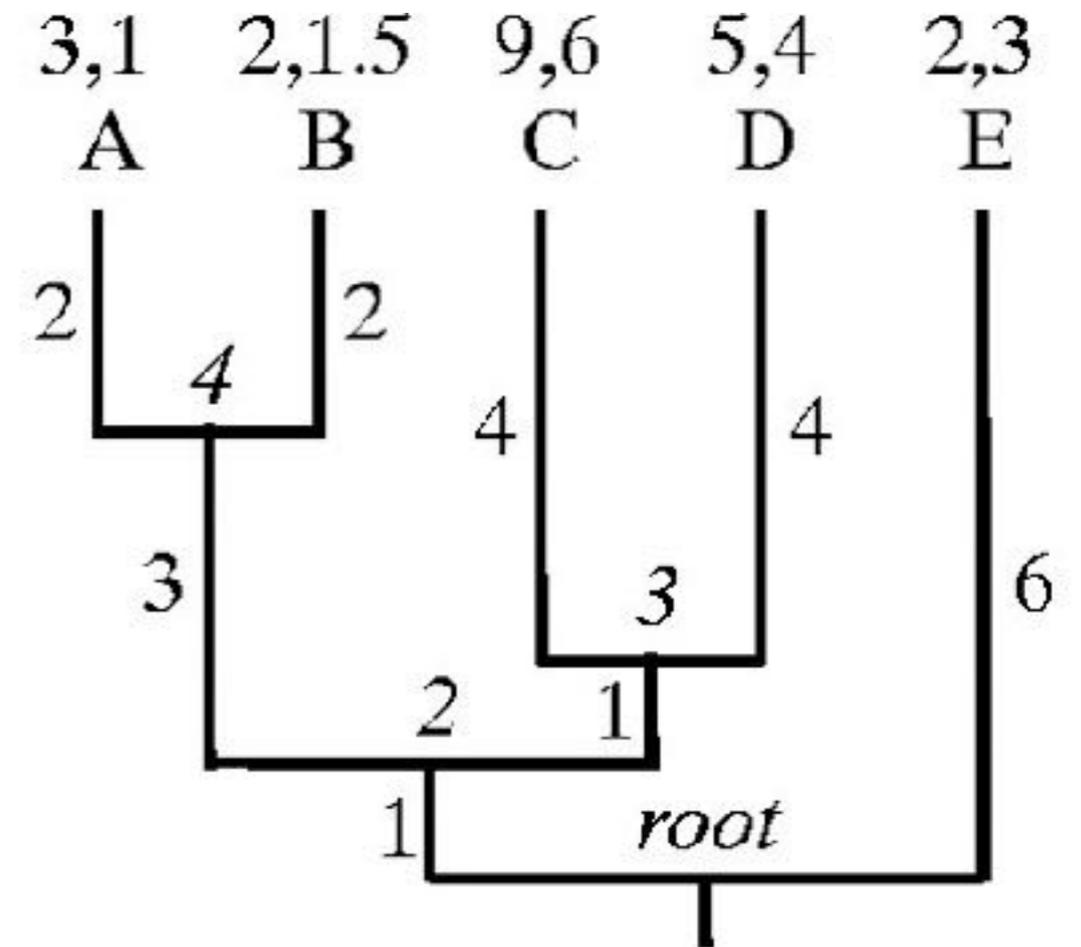
- input: N trait measures (continuous value), tree
- output: $N-1$ **contrasts**
- contrasts can be used in statistical analysis (correlation, regression, ANOVA, etc)

the contrasts algorithm: overview

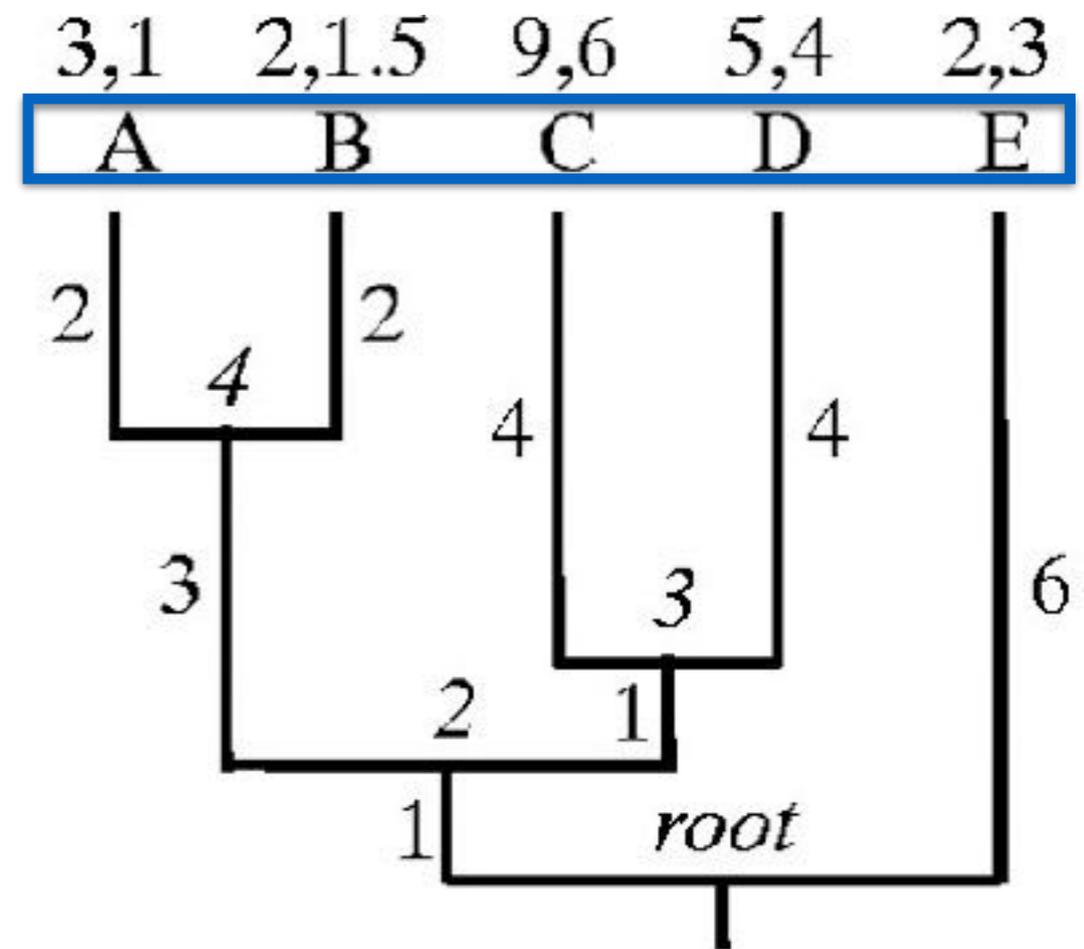
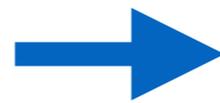
For each internal node....

1. Calculate Raw Contrast
2. Calculate Standardized Contrast
3. Get Expected Trait Value at that node
4. Get Length Correction for Subtending Branch

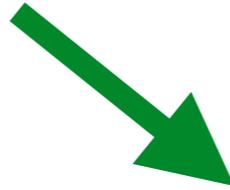
Worked Example



5 species (A-E)



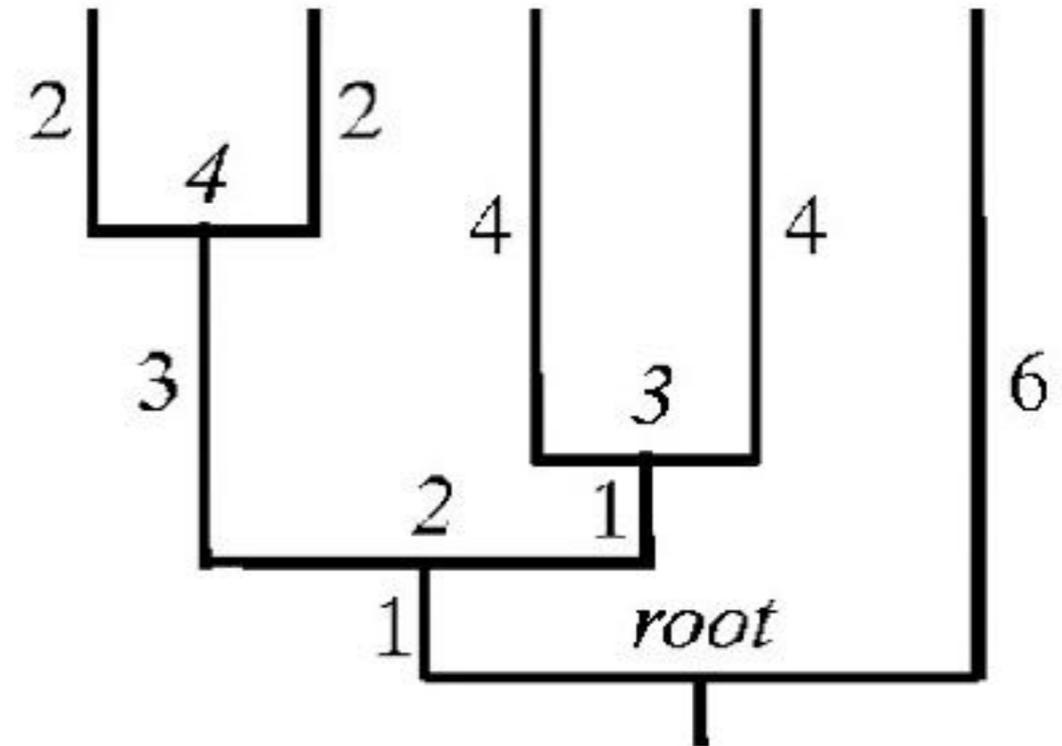
trait values (trait 1, trait 2)



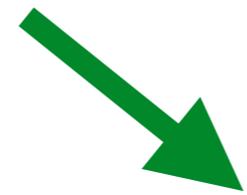
5 species (A-E)



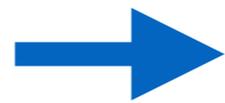
3,1	2,1.5	9,6	5,4	2,3
A	B	C	D	E



trait values (trait 1, trait 2)

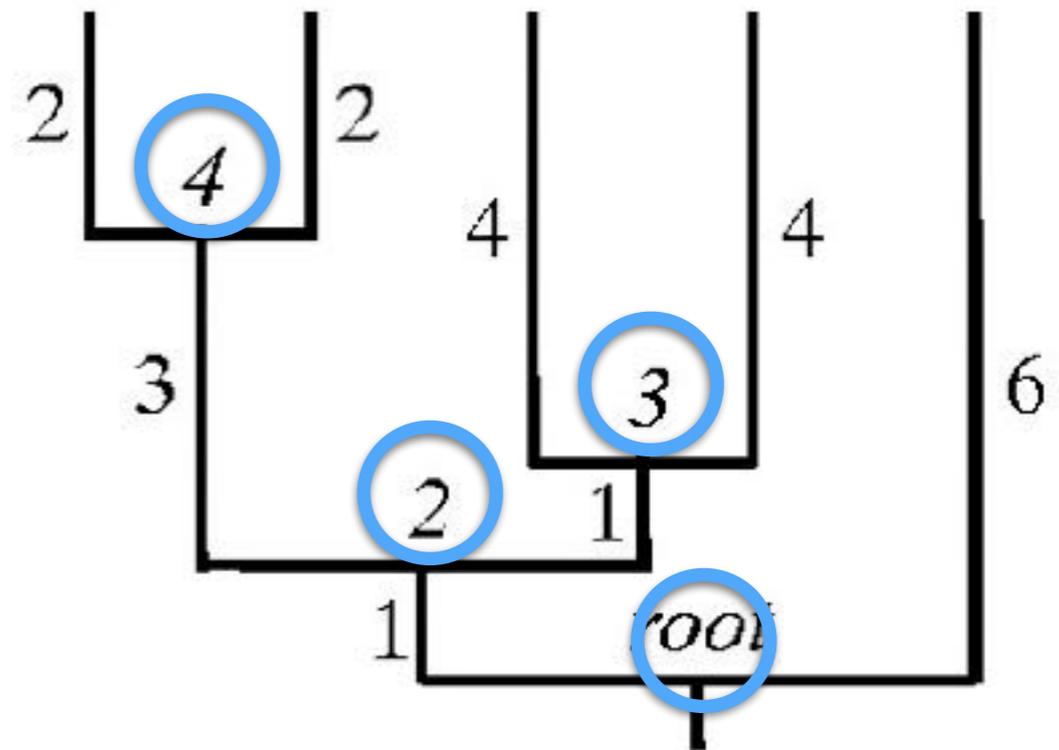


5 species (A-E)



3.1	2.1.5	9.6	5.4	2.3
A	B	C	D	E

4 internal nodes



step 1 get raw contrast

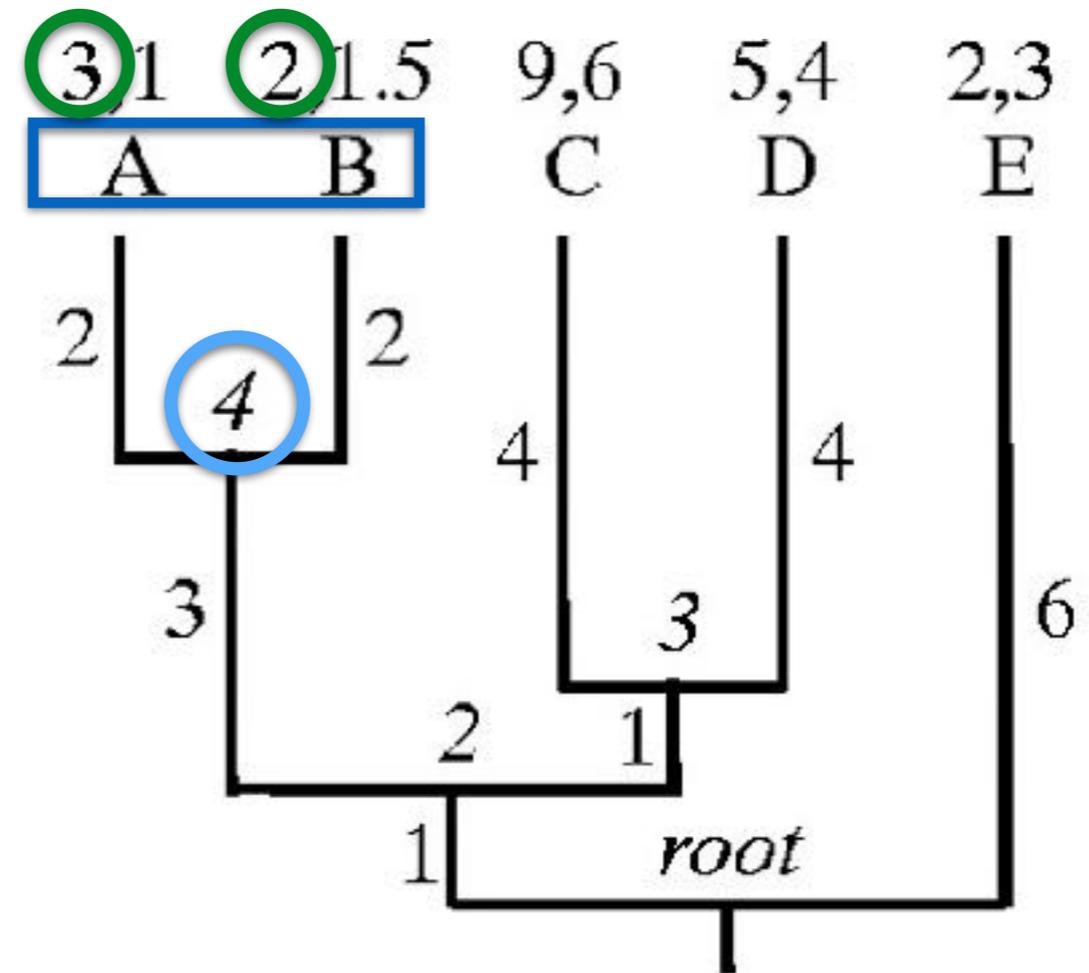
trait values

species

internal nodes

branch lengths

trait 1 raw contrast of node 4: $3 - 2 = 1$



step 2

standardize contrast

$$\text{contrast}_S = \frac{\text{contrast}_R}{\sqrt{\sum \text{branchlengths}}}$$

$$1 / (2 + 2)^{0.5} = 0.5$$

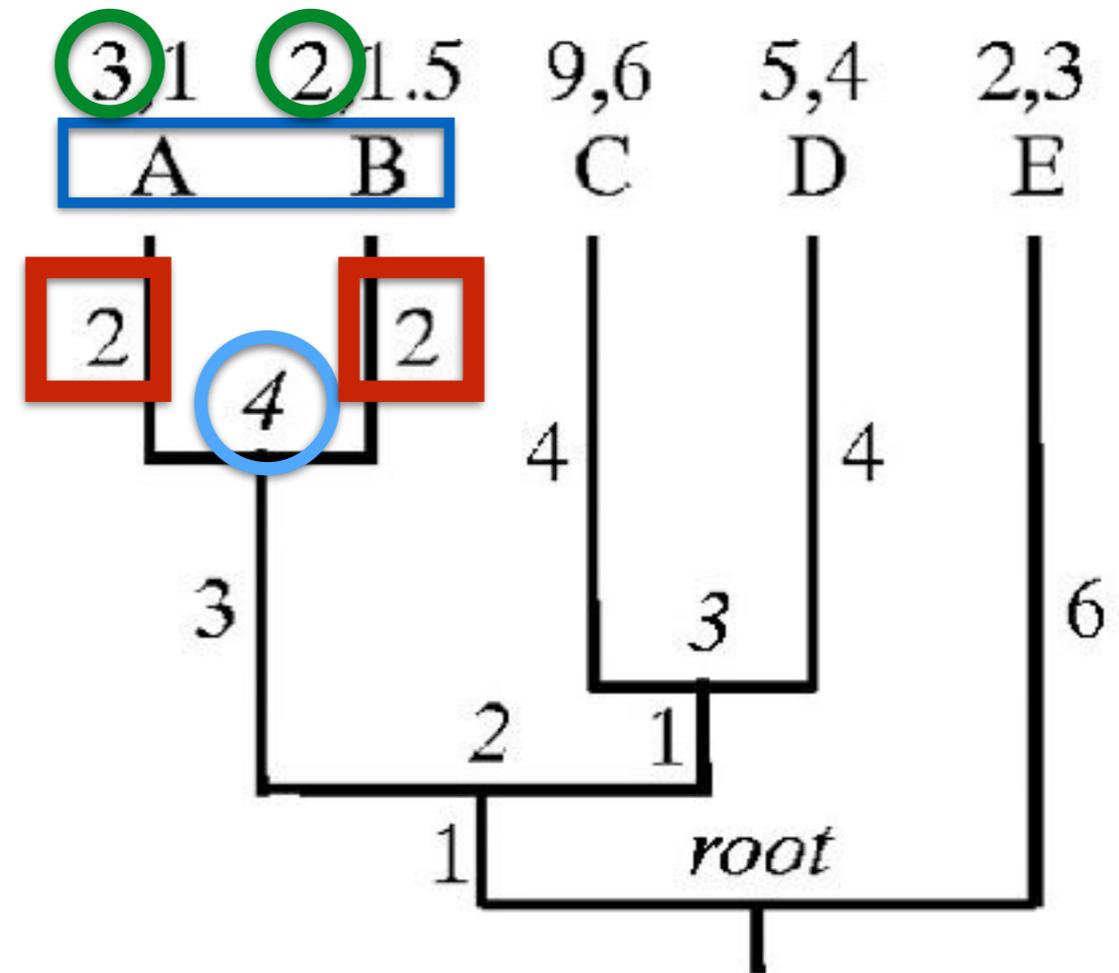
we standardize by amount of branch length since common ancestor to make contrasts comparable to other contrasts

trait values

species

internal nodes

branch lengths



step 2

standardize contrast

$$contrast_S = \frac{contrast_R}{\sqrt{\sum branchlengths}}$$

get the standardized contrast for node 3

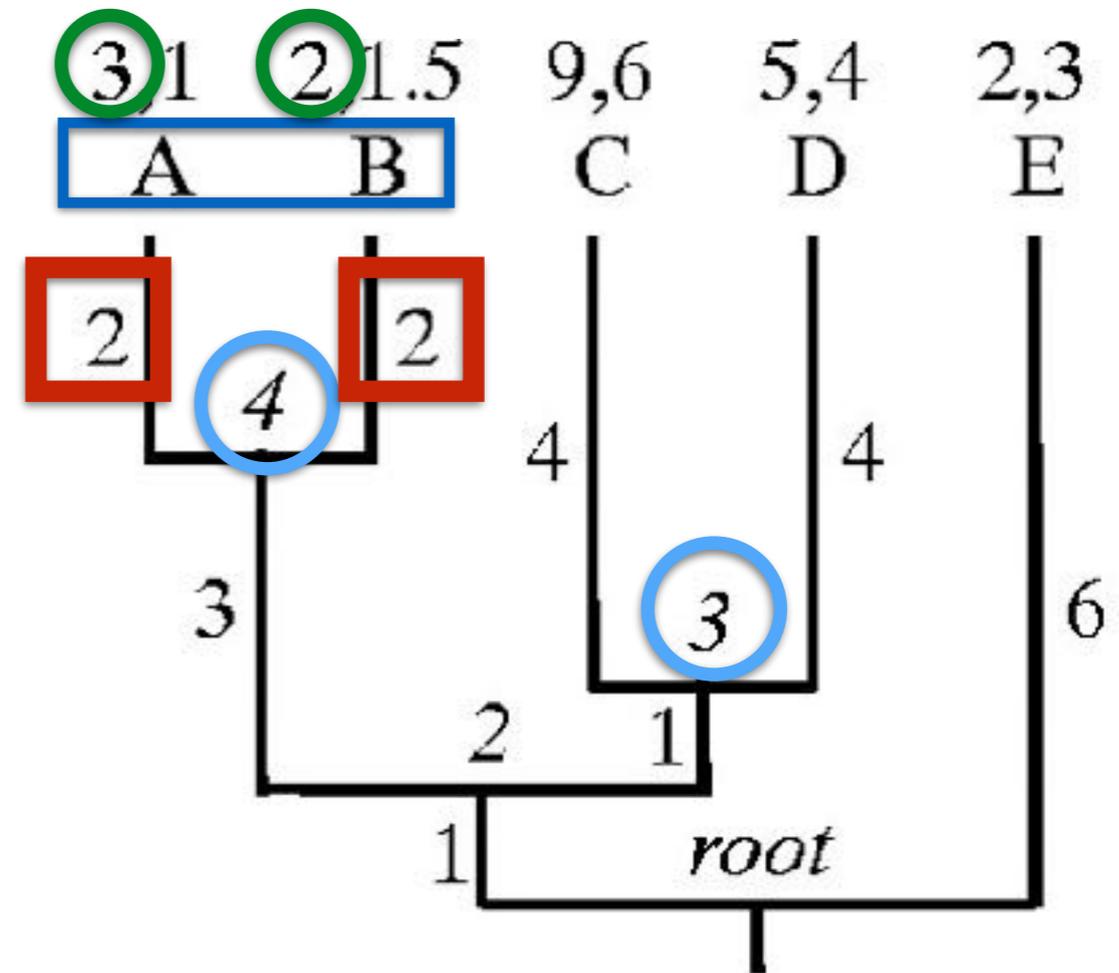
we standardize by amount of branch length since common ancestor to make contrasts comparable to other contrasts

trait values

species

internal nodes

branch lengths



step 2

standardize contrast

$$\text{contrast}_S = \frac{\text{contrast}_R}{\sqrt{\sum \text{branchlengths}}}$$

get the standardized contrast for node 2

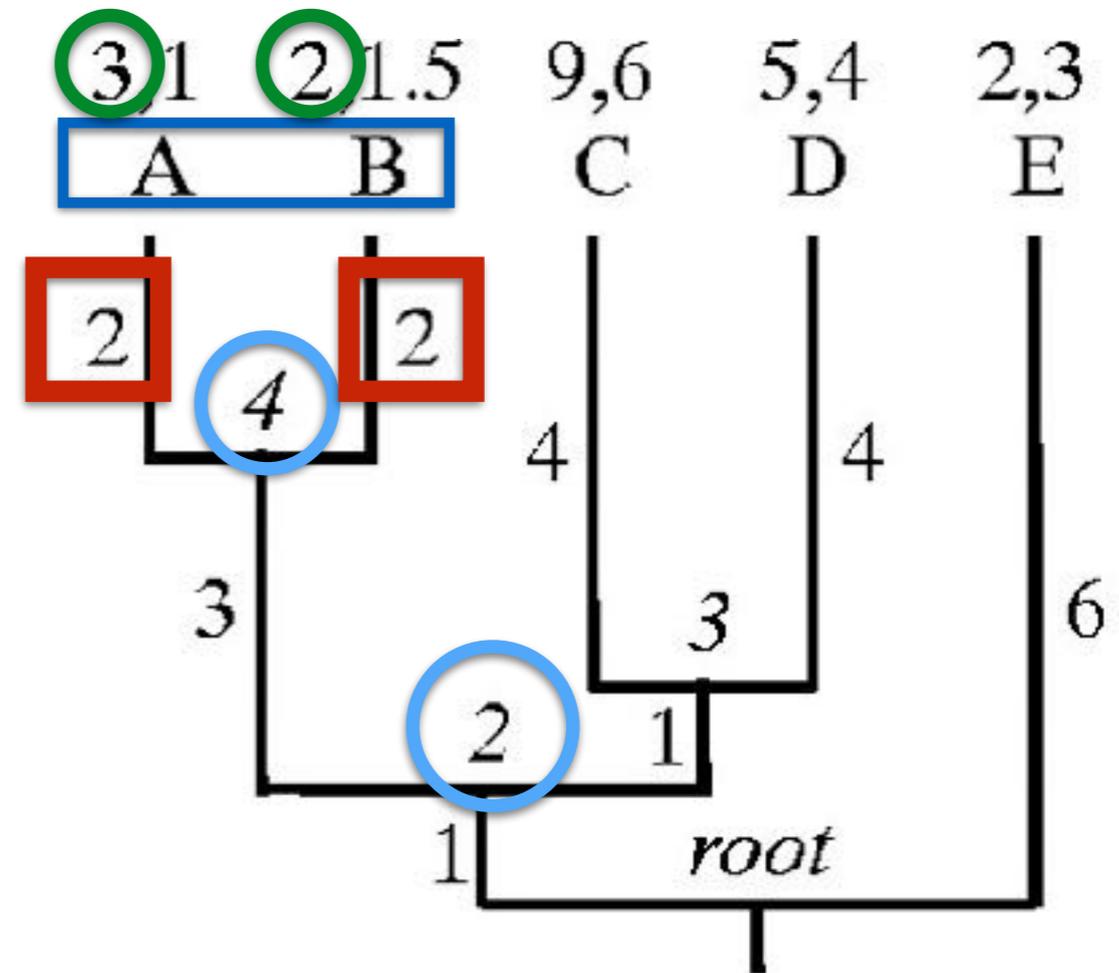
we standardize by amount of branch length since common ancestor to make contrasts comparable to other contrasts

trait values

species

internal nodes

branch lengths



step 2

standardize contrast

$$\text{contrast}_S = \frac{\text{contrast}_R}{\sqrt{\sum \text{branchlengths}}}$$

get the standardized contrast for node 2

(we need to know the trait values for internal nodes)

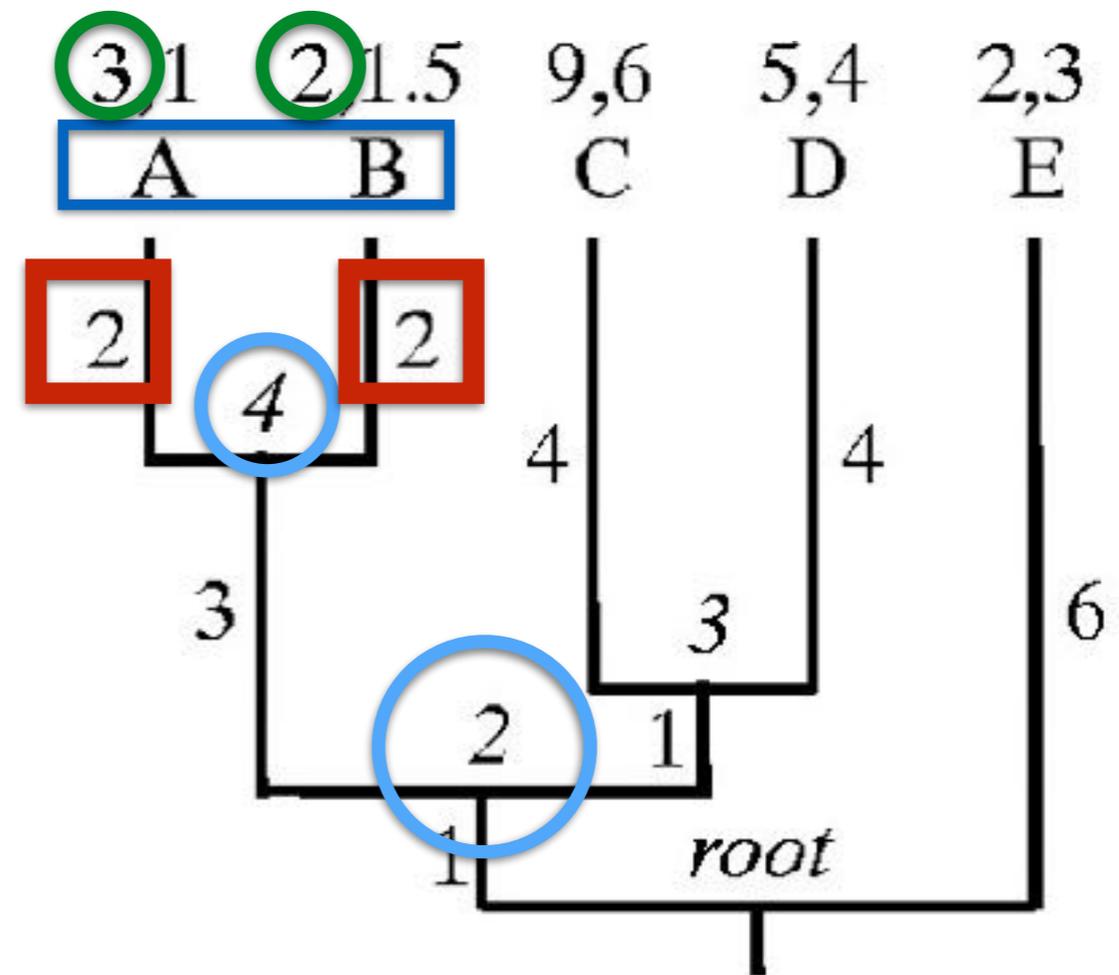
we standardize by amount of branch length since common ancestor to make contrasts comparable to other contrasts

trait values

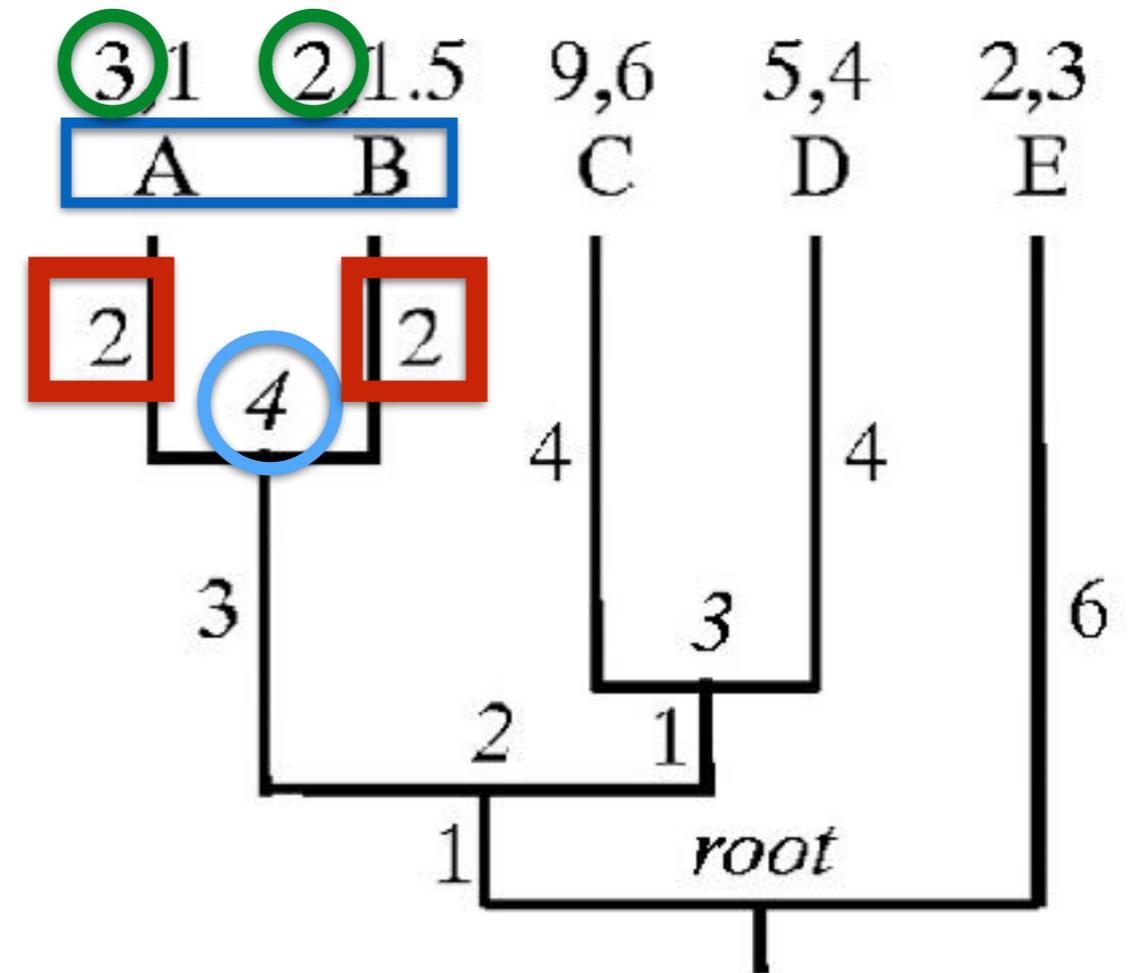
species

internal nodes

branch lengths



Step 3: get internal node value of trait

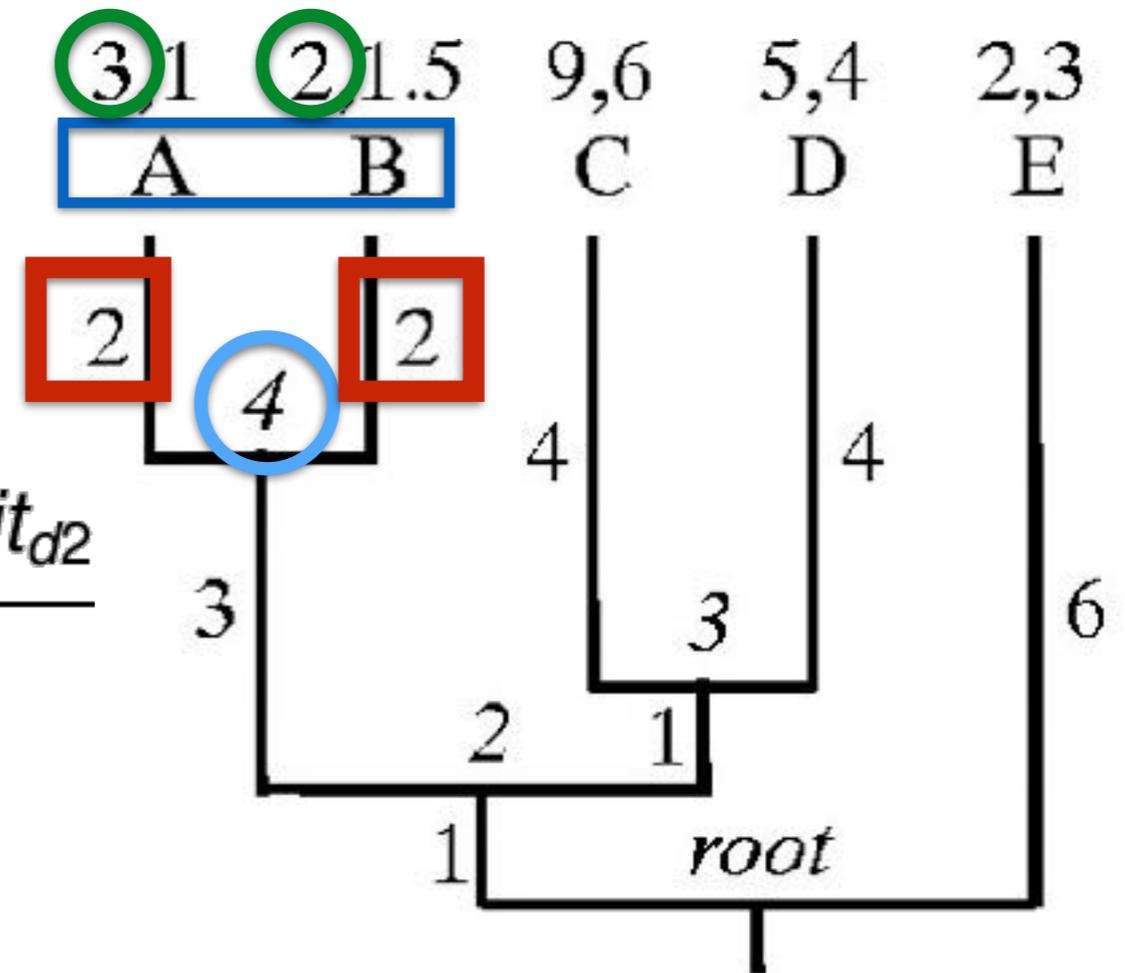


*trait value of the internal node is the average of the trait values in the daughter species **weighted** by branch length*

Step 3: get internal node value of trait

$$trait_{internal} = \frac{\frac{1}{branch_1} * trait_{d1} + \frac{1}{branch_2} * trait_{d2}}{\frac{1}{branch_1} + \frac{1}{branch_2}}$$

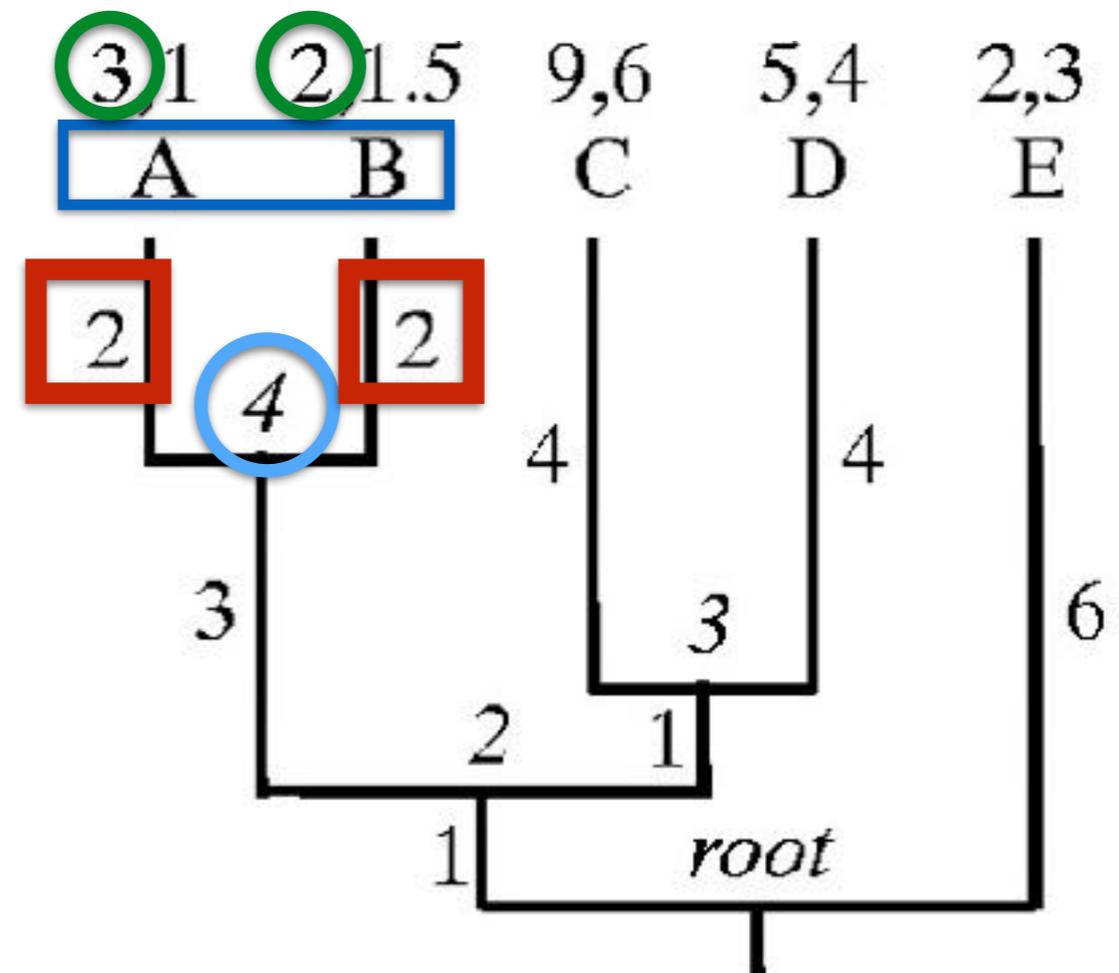
*trait value of the internal node is the average of the trait values in the daughter species **weighted** by branch length*



Step 3: get internal node value of trait

$$\begin{aligned}
 \text{trait}_{\text{internal}} &= \frac{\frac{1}{\text{branch}_1} * \text{trait}_{d1} + \frac{1}{\text{branch}_2} * \text{trait}_{d2}}{\frac{1}{\text{branch}_1} + \frac{1}{\text{branch}_2}} \\
 &= \\
 &= \mathbf{(3/2 + 2/2)/(1/2 + 1/2)} \\
 &= \\
 &= \mathbf{2.5}
 \end{aligned}$$

*trait value of the internal node is the average of the trait values in the daughter species **weighted** by branch length*

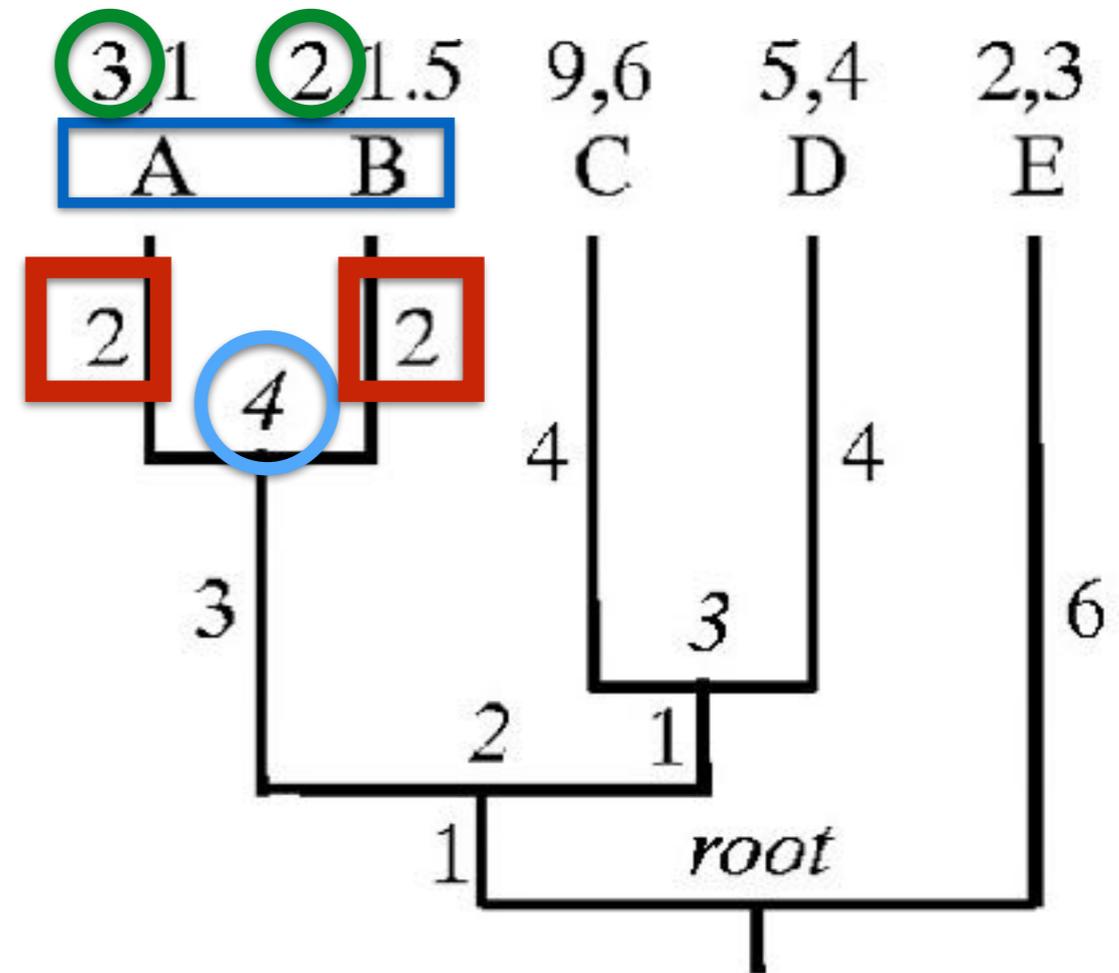


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get internal value of node 3

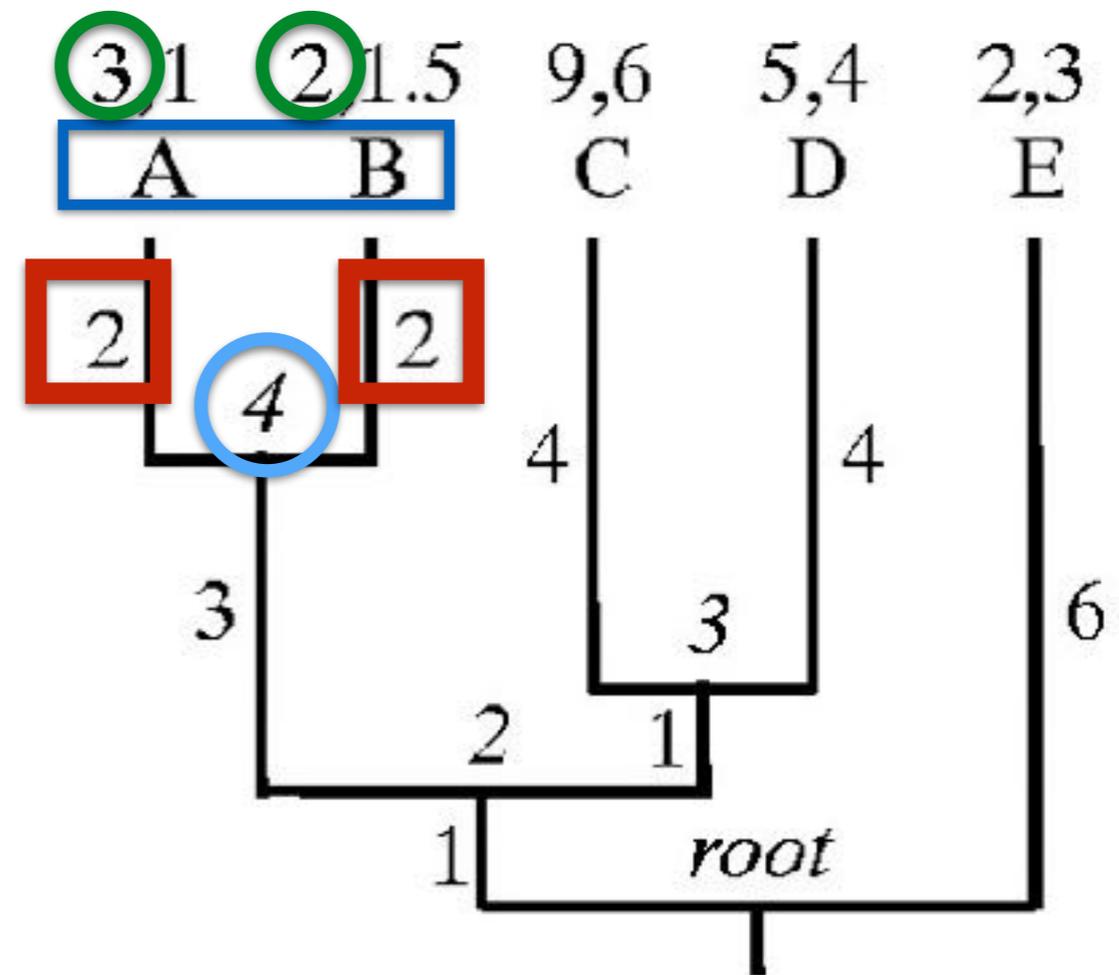
*trait value of the internal node is the average of the trait values in the daughter species **weighted** by branch length*



Step 4: calculate error of branch length leading to interior contrast

$$\text{brancherror} = \frac{\text{branch}_1 * \text{branch}_2}{\text{branch}_1 + \text{branch}_2}$$

error in trait estimation of internal nodes can be expressed as a burst of evolution at that node

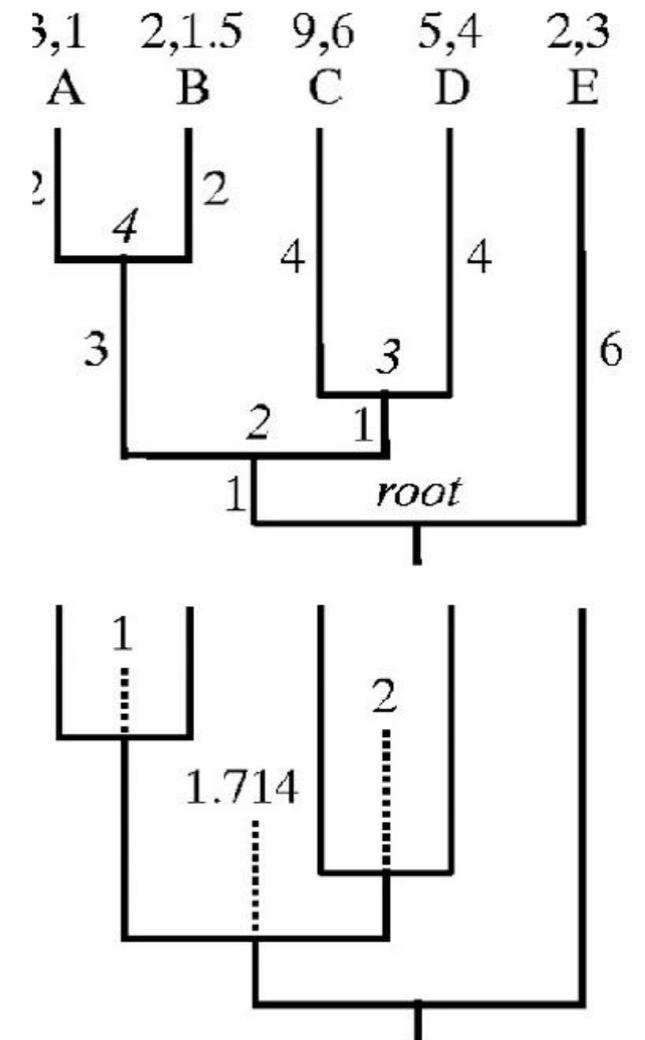


Step 4: calculate error of branch length leading to interior contrast

$$\begin{aligned} \text{brancherror} &= \frac{\text{branch}_1 * \text{branch}_2}{\text{branch}_1 + \text{branch}_2} \\ &= \frac{(2 * 2) / 4}{(2 + 2)} \\ &= 1 \end{aligned}$$

error in trait estimation of internal nodes can be expressed as a burst of evolution at that node

this new length is used for all subsequent calculations using that branch



Exercise: work singly or in pairs, calculate all standardized contrasts for traits 1 and 2 for traits 1 and 2

step 2 (standardize)

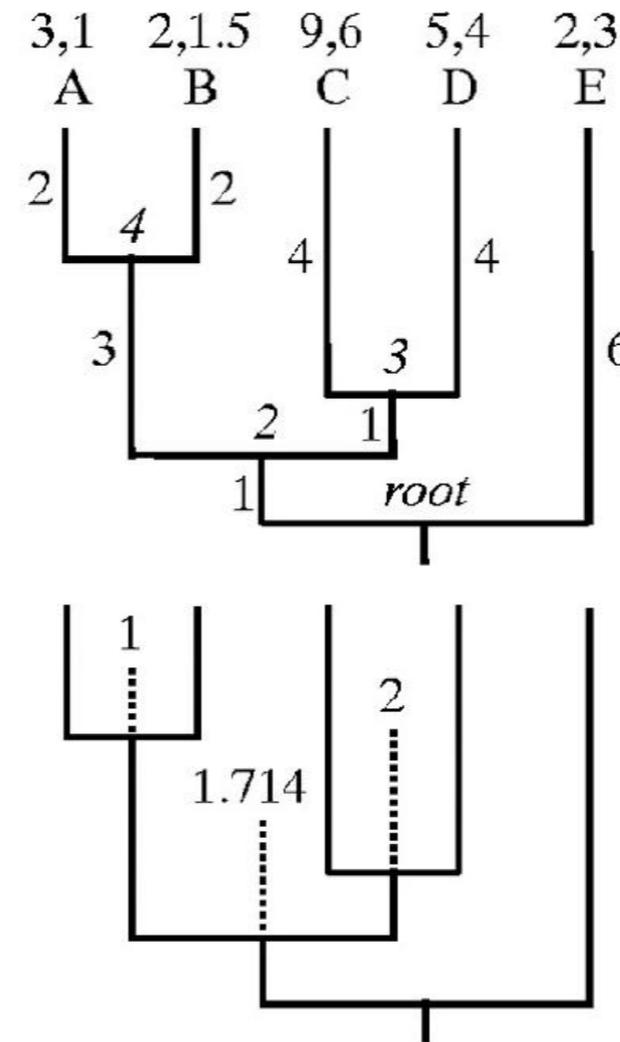
$$\text{contrast}_S = \frac{\text{contrast}_R}{\sqrt{\sum \text{branchlengths}}}$$

step 3 (internal value)

$$\text{trait}_{\text{internal}} = \frac{\frac{1}{\text{branch}_1} * \text{trait}_{d1} + \frac{1}{\text{branch}_2} * \text{trait}_{d2}}{\frac{1}{\text{branch}_1} + \frac{1}{\text{branch}_2}}$$

step 4 (error)

$$\text{brancherror} = \frac{\text{branch}_1 * \text{branch}_2}{\text{branch}_1 + \text{branch}_2}$$



Phylogenetically independent contrasts calculations for trait 1

Node name	Contrast name	Contrast values	Raw contrast	Standard deviation	Standardized contrast	(Corrected) length of each branch	
						Left	Right
4	A-B	3-2	1.0	2.0	0.5	2.0	2.0
3	C-D	9-5	4.0	2.828	1.414	4.0	4.0
2	4-3	2.5-7	-4.5	2.646	-1.701	[4.0]	[3.0]
root	2-E	5.071-2	3.071	2.952	1.040	[2.714]	6.0

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

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$$S_{ij} = \frac{X_i - X_j}{v_i + v_j}$$

What are contrasts?

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$$S_{ij} = \frac{X_i - X_j}{v_i + v_j} \quad \text{“amount of change”}$$

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

$$S_{ij} = \frac{X_i - X_j}{v_i + v_j}$$

“amount of change”
“time”

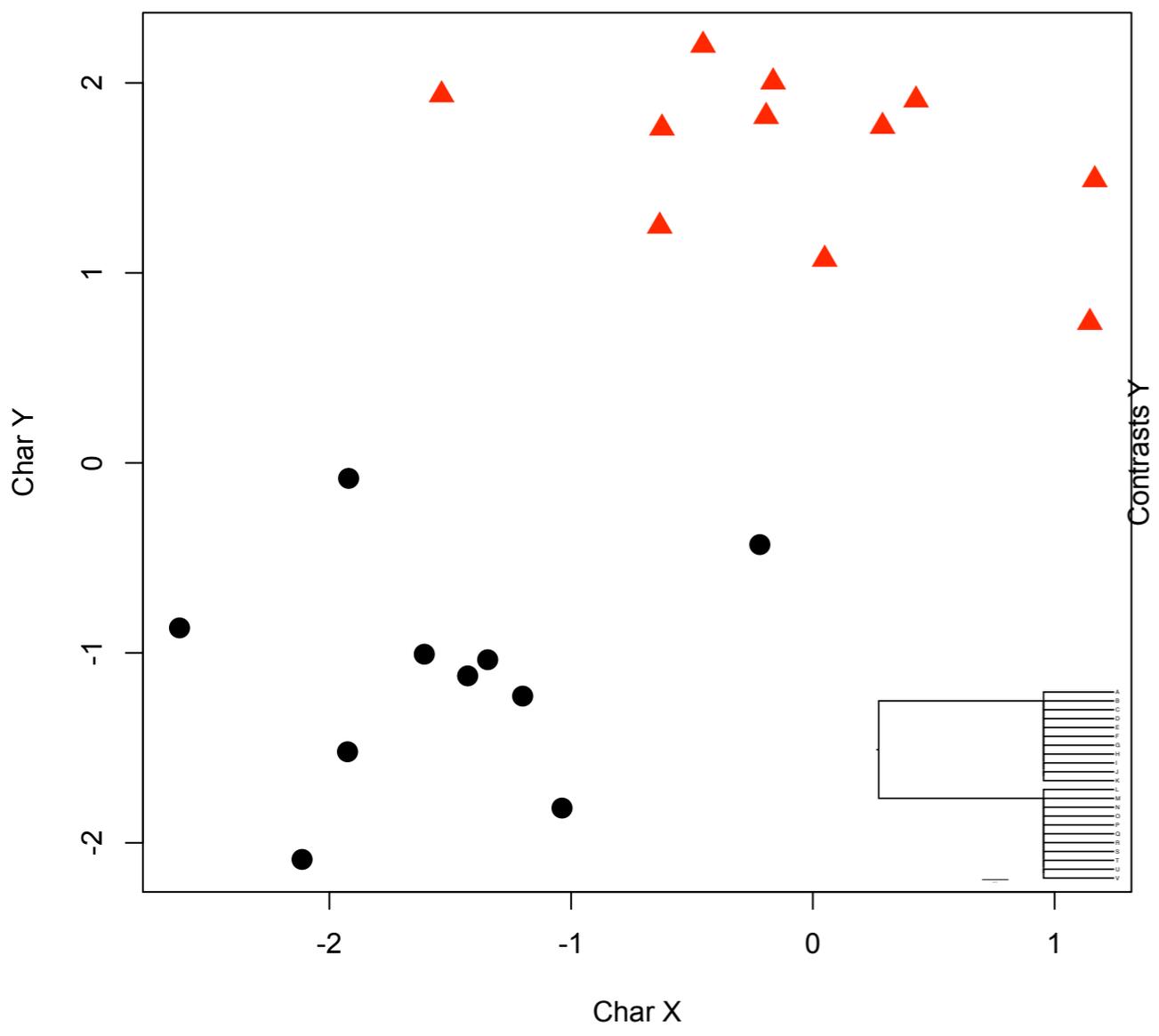
What are contrasts?

- The contrasts have a close relationship with σ^2 , the rate parameter from BM
- The sum of the squared contrasts divided by n gives the ML estimate of σ^2

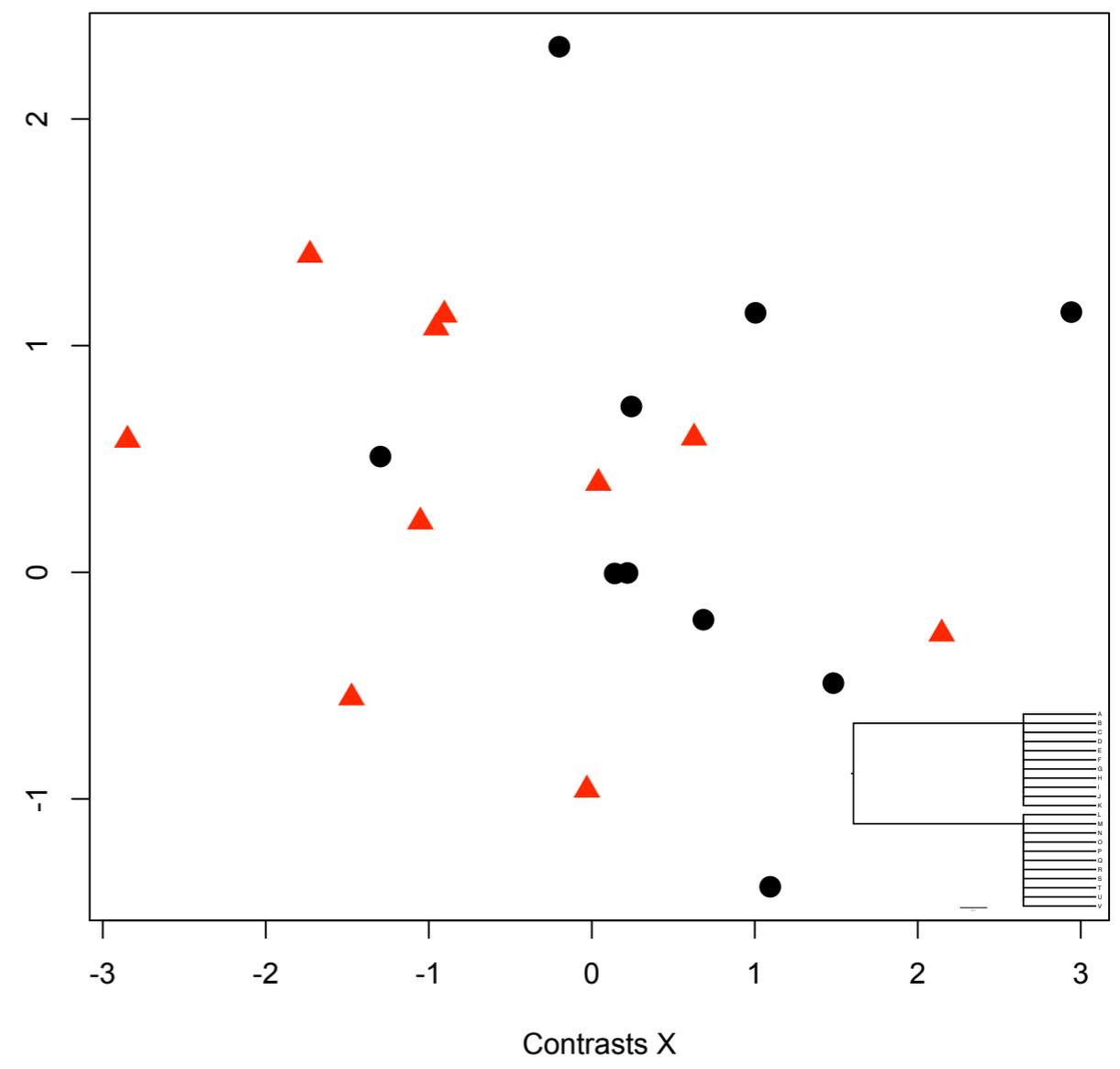
Using and Interpreting Contrasts

- Independent contrasts should be thought of as vectors
- They summarize information about the **amount** and **direction** of evolution at each node in the tree
- Standardized contrasts provide information about the **rate** of evolution

contrasts can then be used in multivariate analyses



RAW data



contrast data

Wrasse Feeding Diversity

Crustacivores



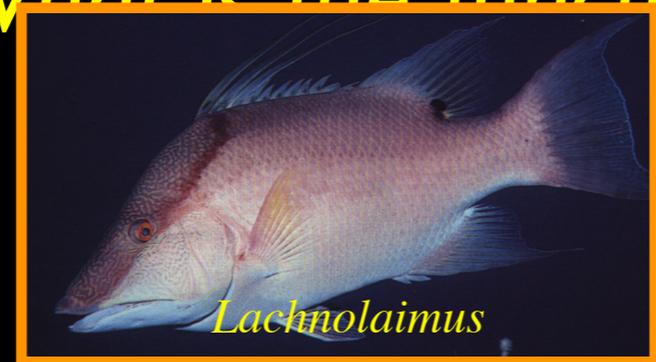
Planktivores



Molluscivores



What is the functional basis of diversity?



Piscivores

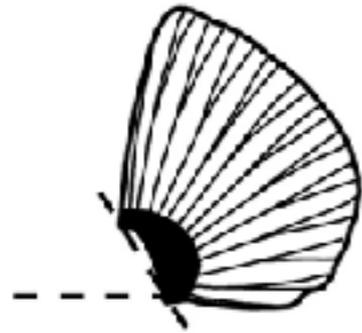


Herbivores



Have skull and pectoral fins evolved together?

(a)

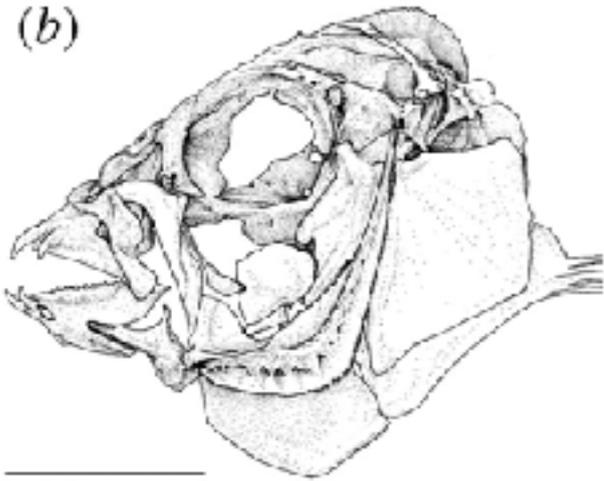


Labropsis australis

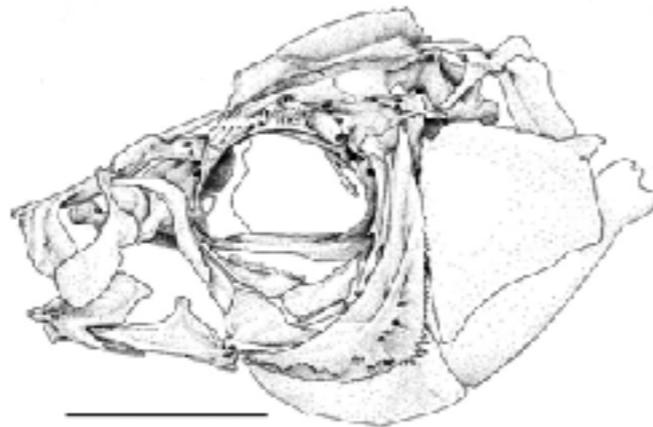


Gomphosus varius

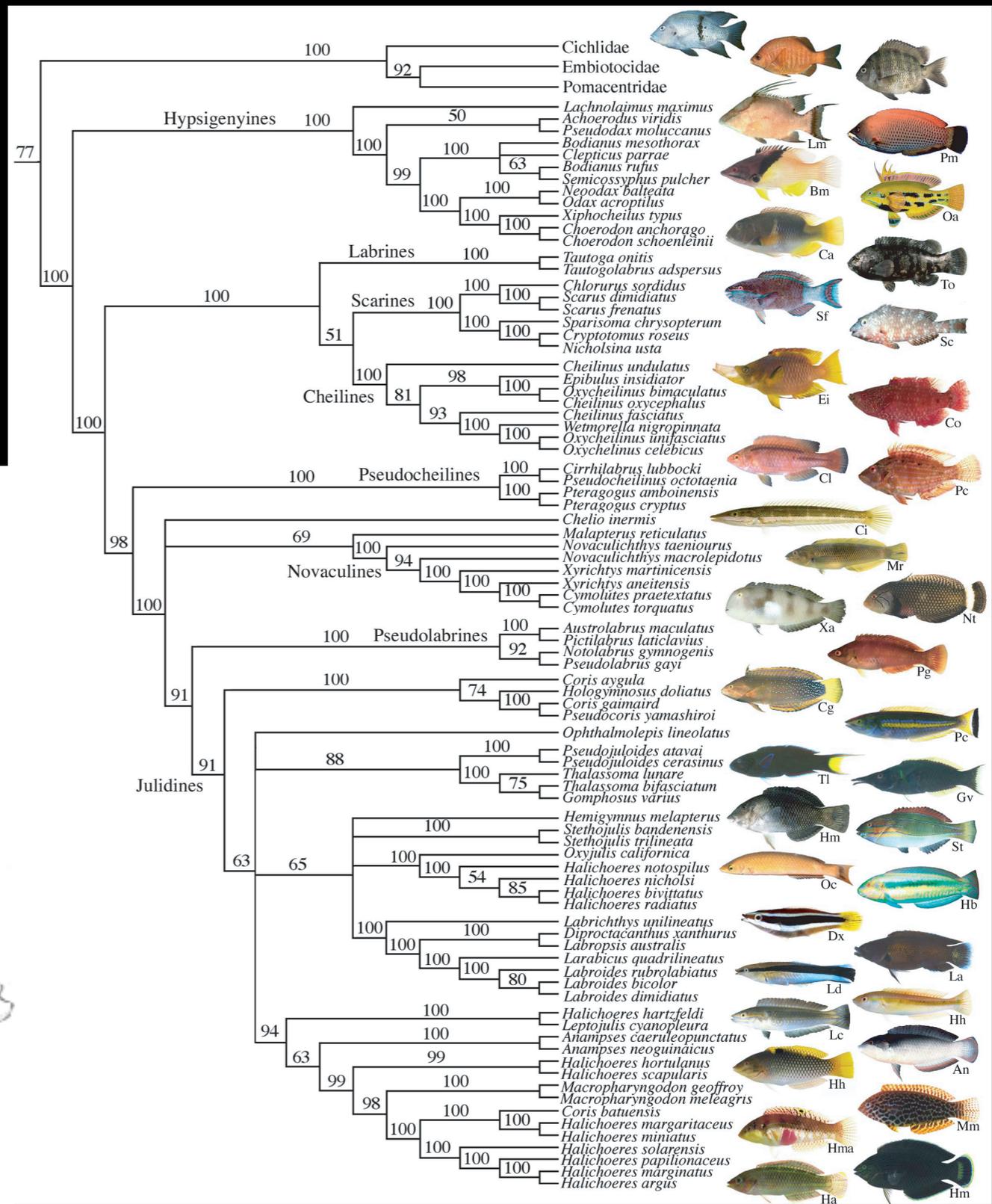
(b)



Choerodon anchorago



Clepticus parrae



Using and Interpreting Contrasts

$$\hat{\sigma}^2 = \frac{\sum S_i}{n-1}$$

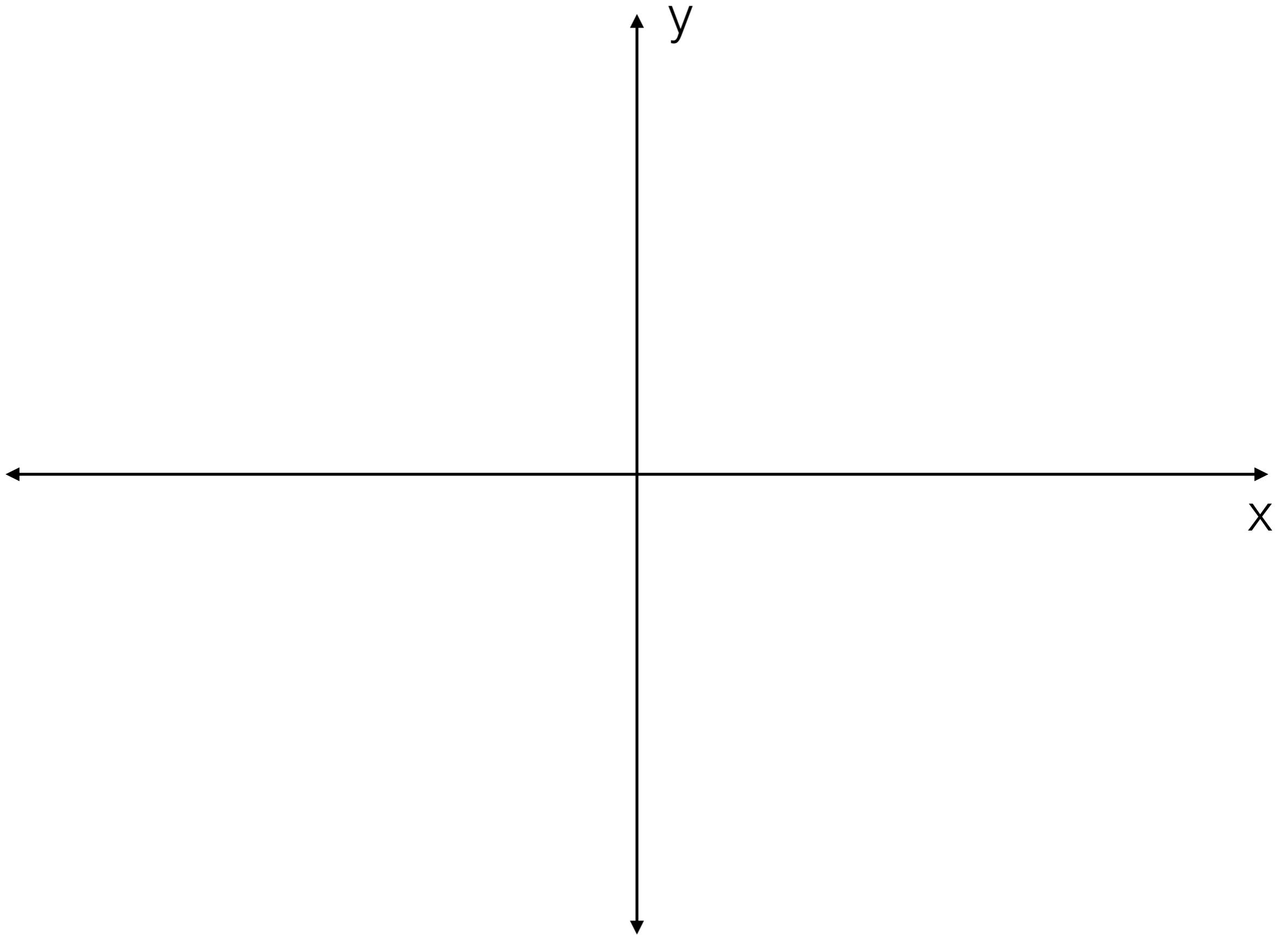
- This provides an unbiased estimate of evolutionary rate
- The expected value of this estimate is equal to the actual rate parameter
- The maximum likelihood estimate of the rate parameter is biased

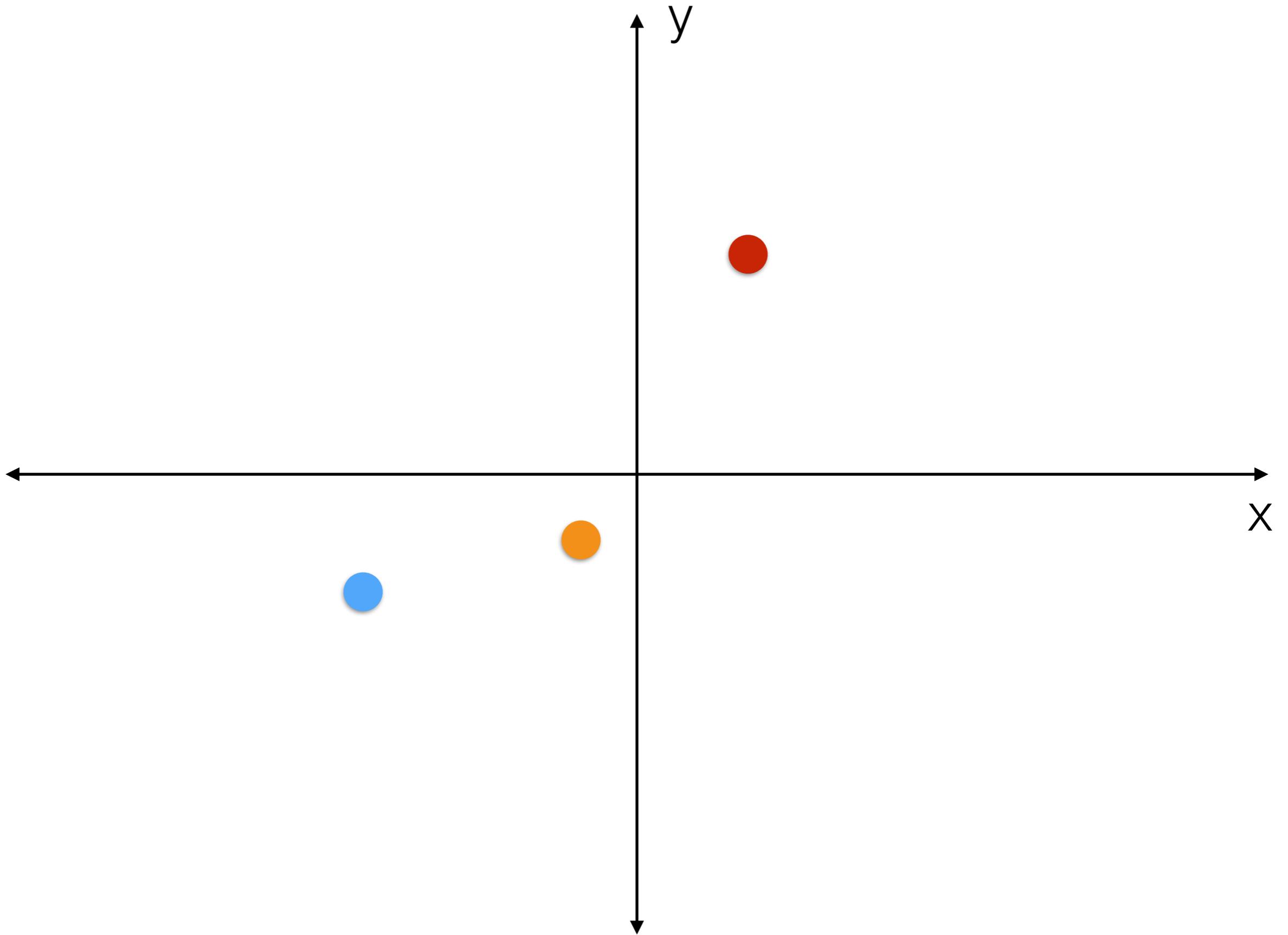
Character correlations

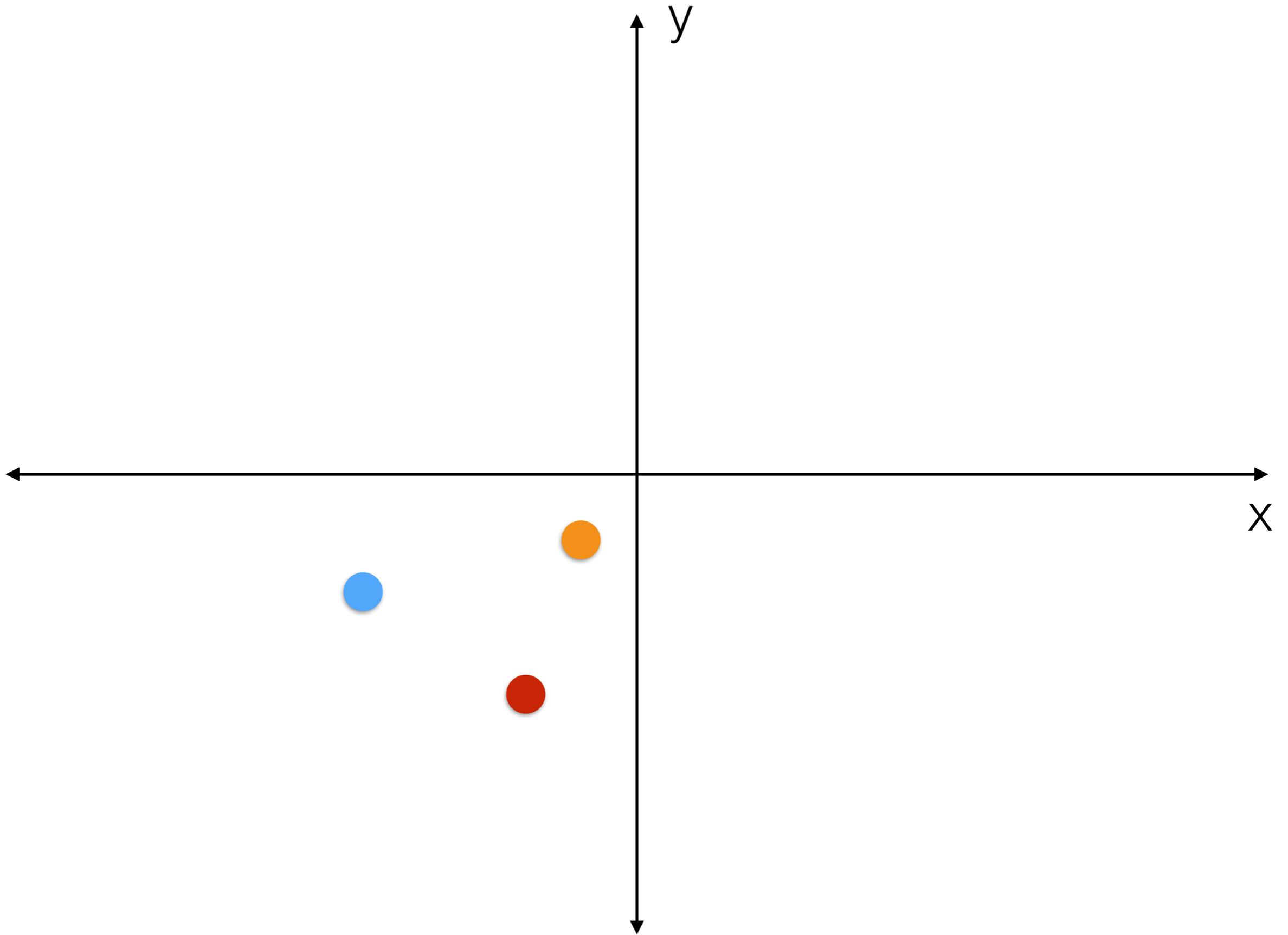
- Most common use for ICs: testing for character correlations
- Are two characters evolving in a correlated fashion?

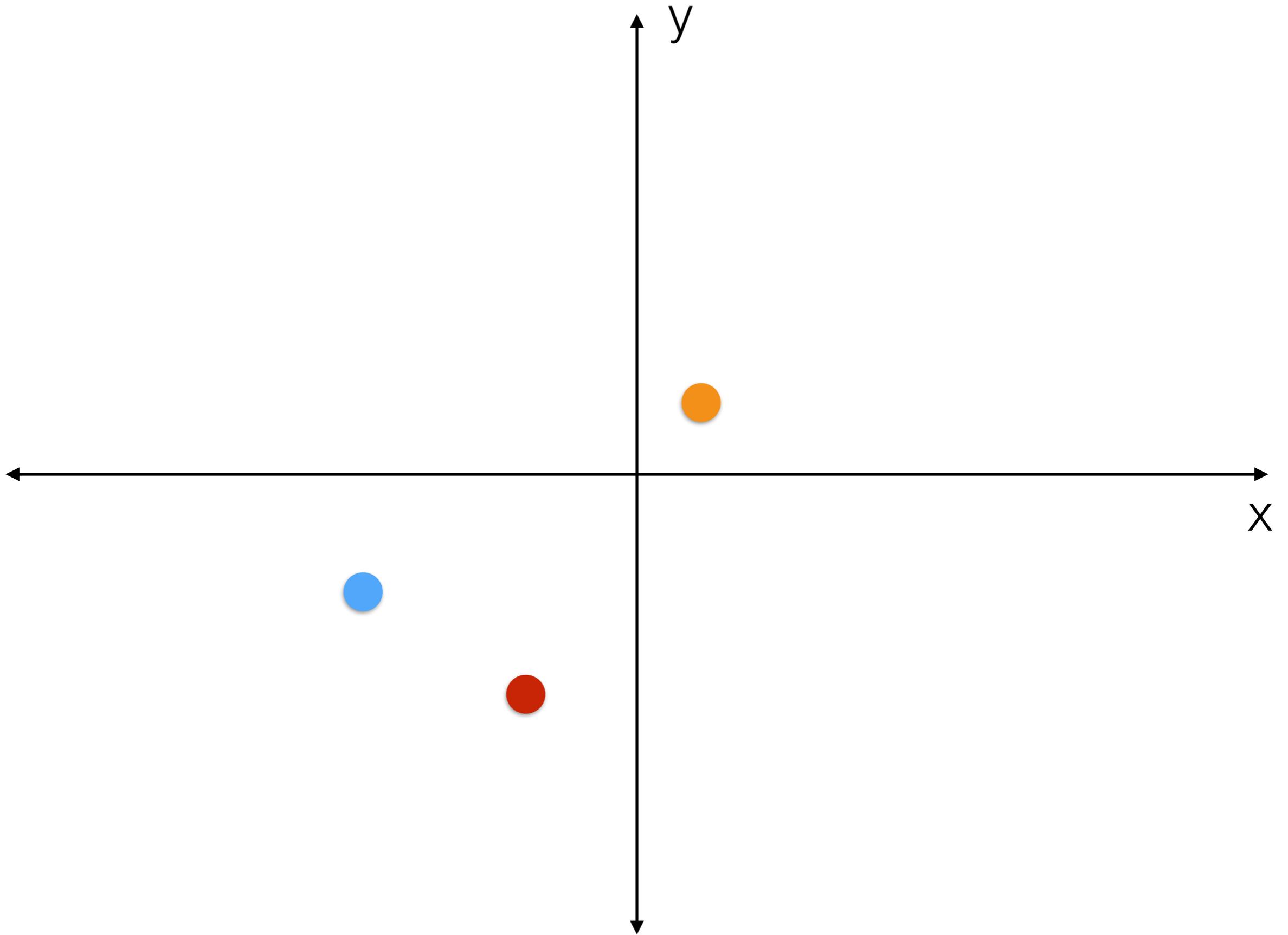
Character correlations

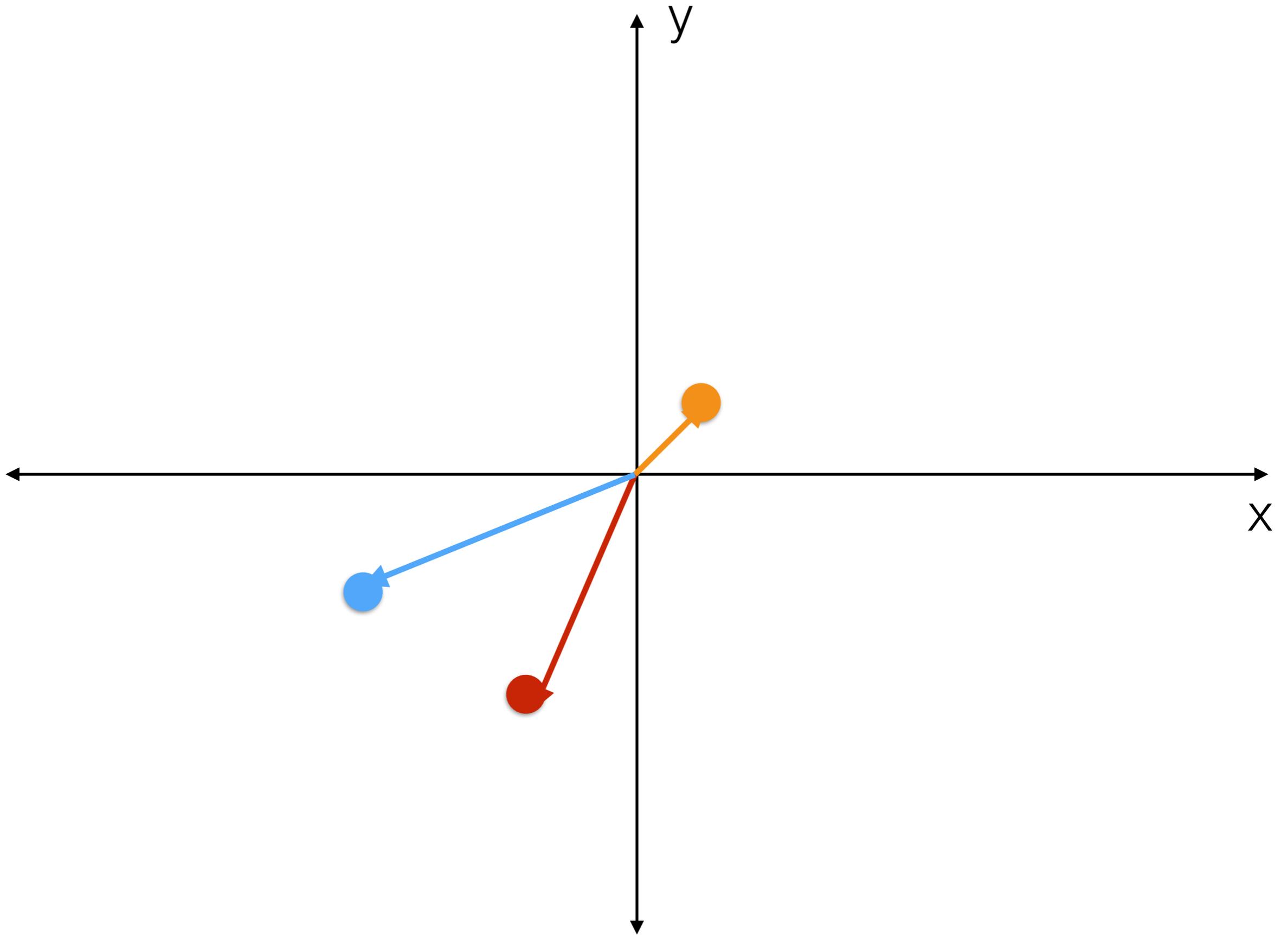
- Calculate independent contrasts for two characters, x and y
- Carry out a regression analysis of y on x with **no intercept** (force regression line through the origin)
- $P < 0.05$, then reject the null hypothesis of no evolutionary correlation

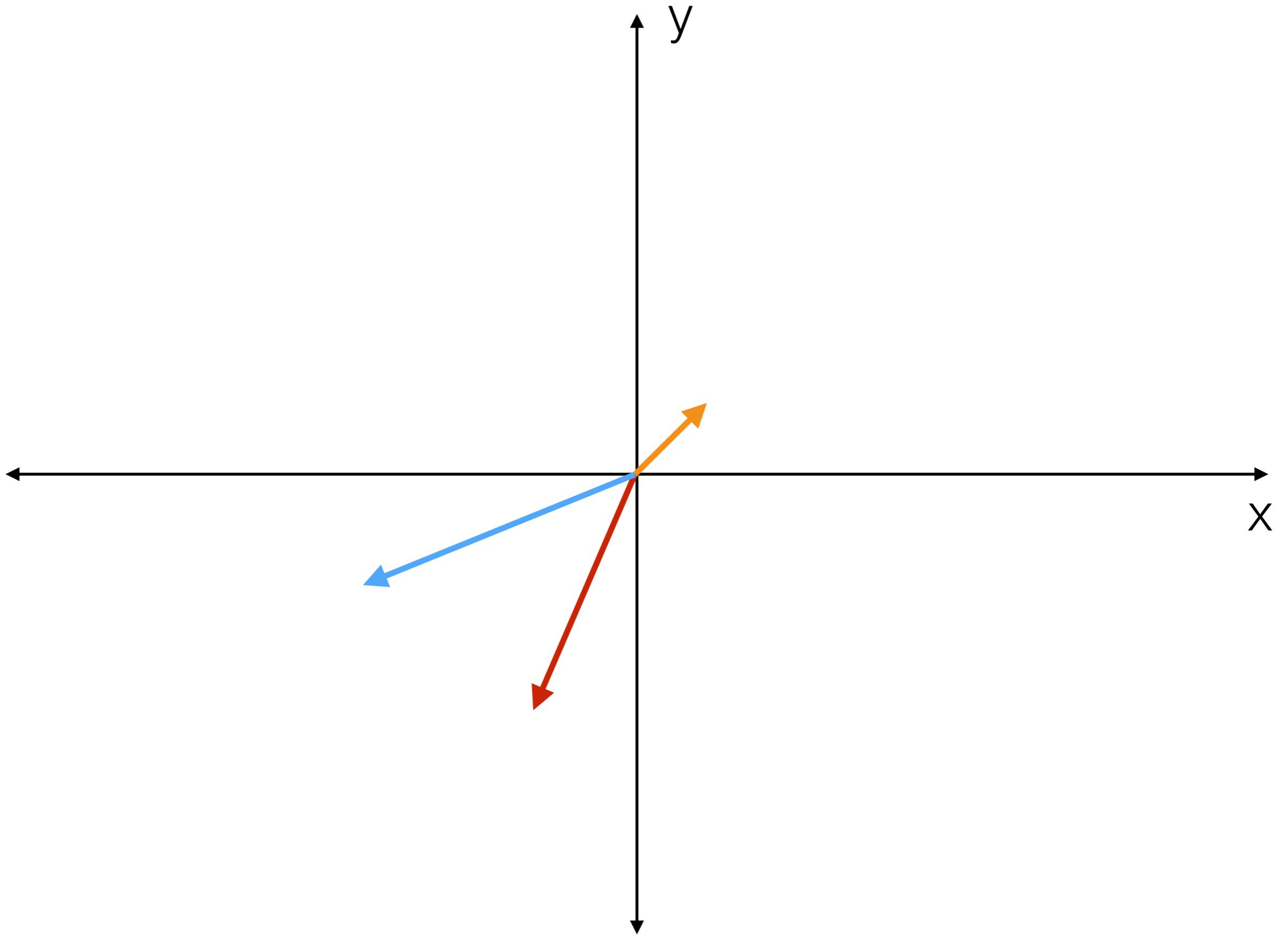


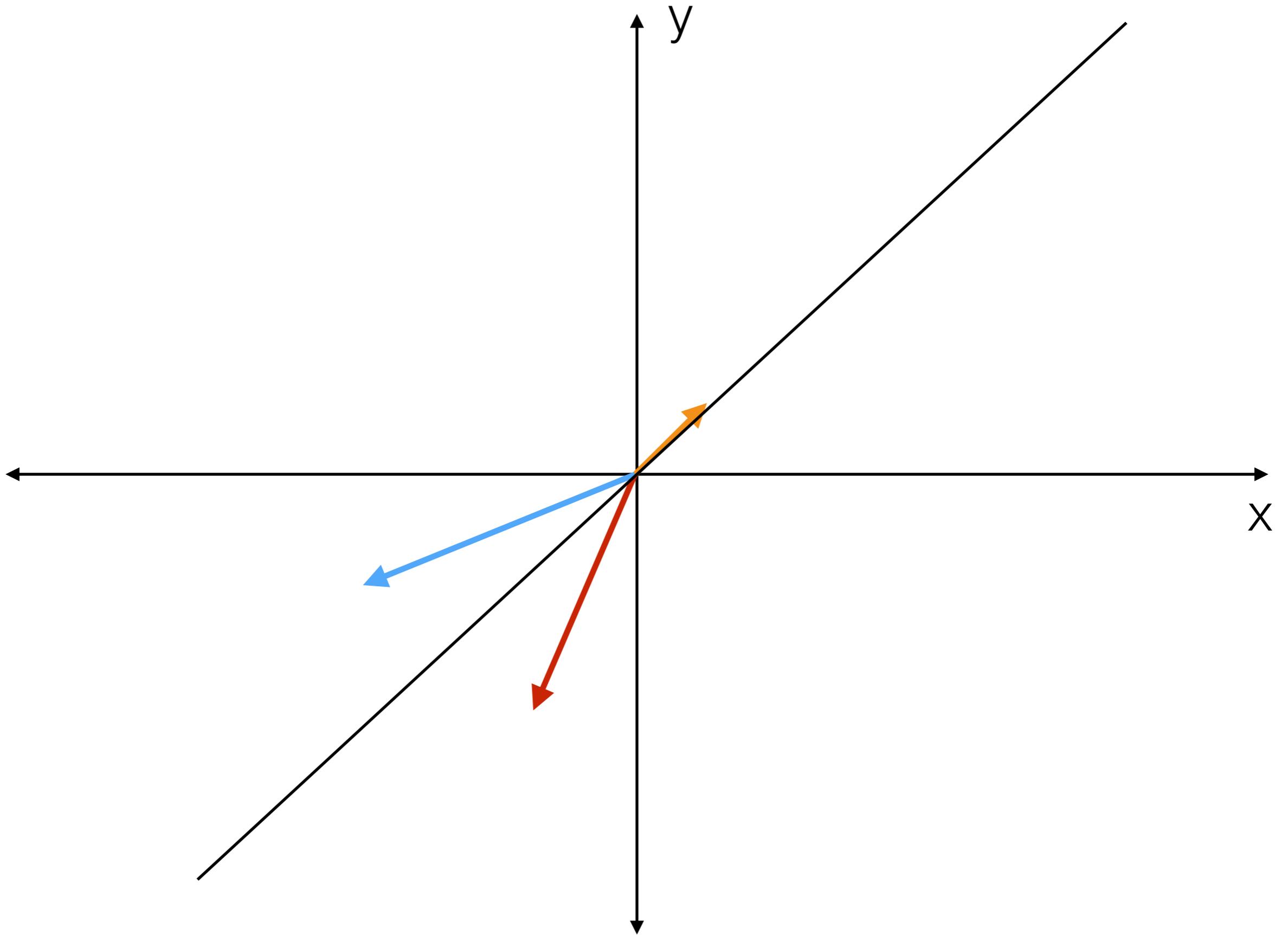










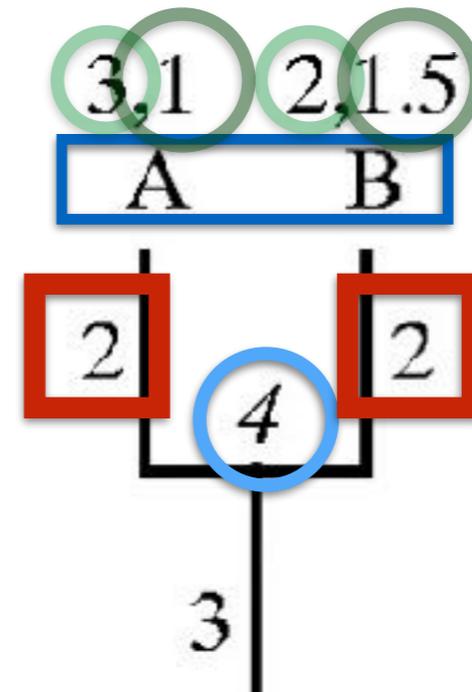


Character correlations

- Why force contrasts through the origin?
- Because, for each contrast, the direction of subtraction is arbitrary; the signs of all the contrasts could be reversed
- Regression through the origin treats the contrasts as vectors
- Biological reason: at node, expected divergence between traits is 0

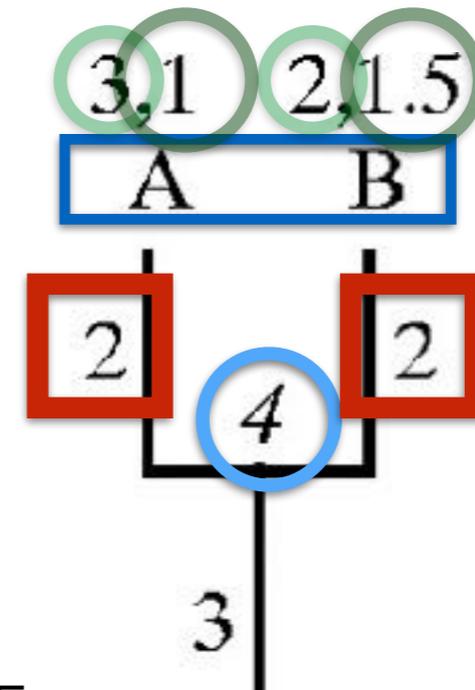
covariation between original traits and trait contrasts does not change

- regression analysis on contrasts allows for tests of correlated evolution
- to preserve covariation, contrasts on traits must be calculated in same order



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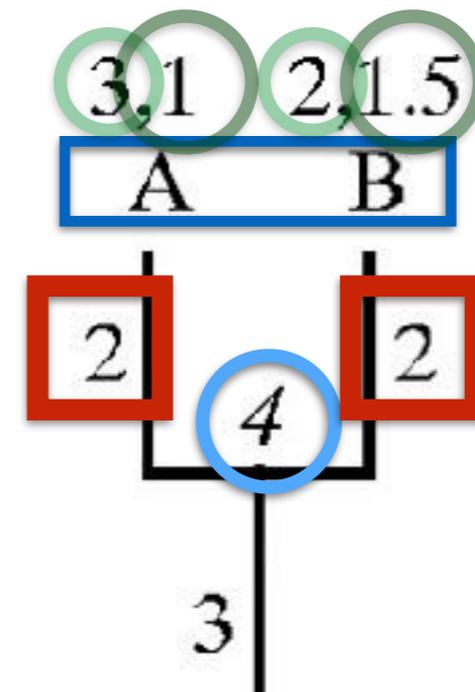


$$\begin{aligned}C1 &= 3-2 = 1 \\C2 &= 1-1.5 = -0.5 \\C1 &= 2-3 = -1 \\C2 &= 1.5-1 = 0.5\end{aligned}$$

yes

covariation between original traits and trait contrasts does not change

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$$C1 = 3 - 2 = 1$$
$$C2 = 1 - 1.5 = -0.5$$

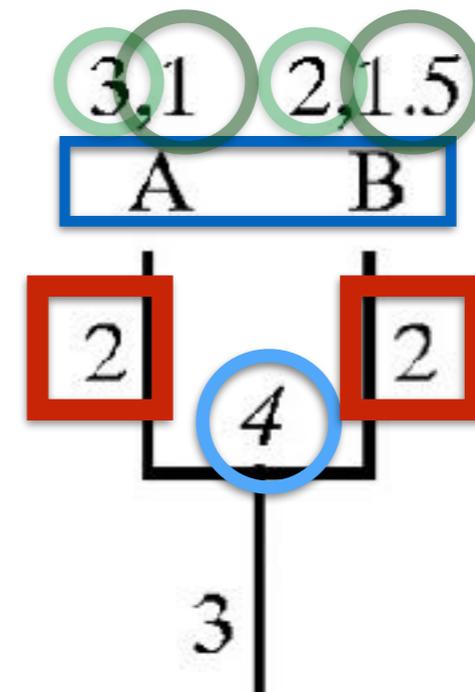
$$C1 = 2 - 3 = -1$$
$$C2 = 1.5 - 1 = 0.5$$

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$$C1 = 3 - 2 = 1$$
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$$C2 = 1.5 - 1 = 0.5$$

yes

~~$$C1 = 3 - 2 = 1$$
$$C2 = 1.5 - 1 = 0.5$$~~

no